SOCIAL INSECTS IN THE TROPICS

Pierre JAISSON
Editor

Volume 2

SOCIAL INSECTS IN THE TROPICS

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SOCIAL INSECTS IN THE TROPICS

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PREFACE

During the last Congress of the International Union for the Study of Social Insects (I.U.S.S.I.), which took place in Wageningen (Holland) in 1977, it was suggested that the next international meeting organized by the Union should take place in a Third-World country and should cover topics more directly related to tropical regions.

The first international symposium «Social Insects in the Tropics» the Proceedings of which are published in these volumes, is the result of that suggestion. This was also the first international meeting on Social Insects to take place in the Western Hemisphere. It required two years of preparation from the time it seemed to me that Mexico was one of the most appropriate countries in which to hold this meeting, and the collaboration of many individuals and scientific and cultural organizations to bring this idea to fruition.

From the outset, the encouragement of Dr. Raúl N. Ondarza, Secretary general of the committees of the Consejo Nacional de Ciencia y Tecnologia (CONACYT), and Dr. Gonzalo Halffter, Director of the Instituto de Ecologia of Mexico city, convinced me that there was a real possibility of organizing this symposium in Mexico. The interest and support of the project by Dr. Edmundo Flores, Director general of the CONACYT, permited the speedy constitution of International and Local Organizing committees, the latter of which was formed from the Board of Directors of the Sociedad Mexicana da Entomologia. The President of this Society, Dr. José-Luis Carrillo, played a critical role in the local committee's coordination. He also partipated in the scientific work of the international organizing committee with Drs. R.N. Ondarza and Enkerlin (Mexico), and Professors C.D. Michener, President of I.U.S.S.I. (U.S.A.), and P.E. Howse, Secretary general of I.U.S.S.I. (Great Britain) who gave his support to the project from the start. The active support of all these individuals was determinant for the success of the symposium.

Nothing would however have been possible without the material support of various national and international institutions. The CONACYT was particularly helpful and we would like to thank this organization on behalf of the scientific community. Other institutions we would like to thank are the Universidad Nacional Autonoma and the Instituto Politecnico

Nacional of Mexico, the Instituto Nacional de Investigaciones Agrícolas and the Colegio de Postgraduados en Agricultura who organized an international training course on social insects.

We are grateful for the collaboration of the Instituto de Ecologia, the Centro de Investigaciones Ecológicas del Sureste (CIES) and the Instituto Nacional de Investigaciones Sobre Recursos Bióticos, and also of UNESCO who provided some assistance.

The cooperation by these different organizations helped to make possible the publication of the Proceedings of the symposium, as was the collaboration and effort of the 5th Circonscription of the French Centre National de la Recherche Scientifique and the Université Paris XIII.

It is obviously impossible by this means to faithfully reproduce the richness of the discussions between the researchers of 14 different countries. However, we hope that these two volumes, with their 34 contributions, divided according to general topics or by species (as for the round table organized by Professor Michener on the africanized Honeybee), will constitute a basic reference source for present and future investigators of tropical social insects. This is the first specialized international work on this topic. It was produced without any commercial motivation, which permited the reduced sale-price. The financial proceeds will be used for the purpose of organizing other new scientific meetings.

Finally, we are particularly grateful for the cooperation of the 51 specialists, authors of the works that are included in these volumes.

February, 15th, 1982

Pierre Jaisson
Professor at the University Paris XIII
President of the French Section of
I.U.S.S.I.

PRÉFACE

Lors du dernier congrès de l'Union Internationale pour l'Etude des Insectes Sociaux (U.I.E.I.S.) qui s'est tenu en 1977 à Wageningen (Pays-Bas), fut exprimé le souhait qu'une prochaine manifestation internationale, organisée sous l'égide de l'Union, puisse se tenir dans un pays du Tiers-Monde et sur des problèmes intéressant plus directement les zones tropicales.

Le premier symposium international «Insectes Sociaux sous les Tropiques» – dont les comptes rendus sont rassemblés dans cet ouvrage – est la matérialisation de cette volonté. C'est également le premier colloque international sur les sociétés d'insectes à se tenir dans le nouveau monde. Deux années d'efforts ainsi que le concours de nombreuses personnalités et organisations scientifiques ou culturelles furent nécessaires pour aboutir à ce résultat, à partir du moment où il m'avait semblé que le Mexique était l'un des pays les mieux placés pour accueillir cette manifestation.

Dès le début du projet les encouragements du Docteur Raúl N. Ondarza, Secrétaire général des Comités du Consejo Nacional de Ciencia y Tecnología (CONACYT), et du Docteur Gonzalo Halffter, Directeur de l'Instituto de Ecología de Mexico, m'ont démontré que la possibilité existait effectivement d'organiser cette réunion scientifique au Mexique. L'intérêt et l'appui du Docteur Edmundo Flores, Directeur général du CONACYT, permirent d'aboutir rapidement à la constitution d'un Comité International et d'un Comité Local d'Organisation issu du Conseil de Direction de la Société Mexicaine d'Entomologie. L'action du Docteur José-Luis Carrillo, Président de cette Société, fut déterminante au niveau de la coordination du Comité local. Il participa également aux travaux du Comité International avec les Docteurs R.N. Ondarza et D. Enkerlin (Mexique), les Professeurs C.D. Michener, Président de l'U.I.E.I.S. (Etats-Unis) et P.E. Howse, Secrétaire général de l'U.I.E.I.S. (Royaume-Uni) lequel, dès le départ, apporta son soutien au projet. Toutes ces personnalités qui ont donné leur concours actif, sont responsables de la réussite du symposium.

Mais rien n'aurait été possible sans le soutien matériel d'institutions nationales ou internationales. En particulier, l'appui du CONACYT a été déterminant et nous lui témoignons ici notre reconnaissance au nom de la communauté scientifique, de même qu'à l'Universidad Nacional Autonoma et à l'Instituto Politécnico Nacional du Mexique, à l'Instituto Nacional de Investigaciones Agrícolas et au Colegio de Post-graduados en Agricultura, lequel organisa à cette occasion un cours international sur les insectes sociaux.

Nous remercions également l'appui de l'Instituto de Ecología, du Centro de Investigaciones Ecológicas del Sureste (CIES) et de l'Instituto Nacional de Investigaciones sobre Recursos Bióticos, ainsi que l'UNESCO, qui nous apporta son aide.

C'est grâce à ces différents concours qu'a pu être envisagée l'édition des comptes rendus du symposium, mais également grâce à la collaboration du Centre National de la Recherche Scientifique (5ème Circonscription) et de l'Université Paris XIII.

Il est évidemment impossible de traduire, dans toute leur richesse, sous la forme d'un tel ouvrage, les discussions qui se sont déroulées entre les chercheurs de 14 pays différents. Cependant nous espérons que ces deux volumes, qui rassemblent 34 contributions réparties par thèmes généraux ou par thèmes d'espèces (cas de la table ronde sur l'Abeille africanisée, organisée par le Professeur Michener) constituent une référence pour les chercheurs actuels et à venir intéressés par les insectes sociaux tropicaux. Il s'agit du premier ouvrage spécialisé de niveau international existant sur ce thème. Il a été réalisé sans aucun but lucratif, ce qui a permis de déterminer un prix de vente particulièrement intéressant. Les produits de la vente serviront à l'organisation d'autres réunions scientifiques.

Je terminerai cette préface en remerciant tout particulièrement de leur concours les 51 spécialistes auteurs des articles contenus dans cette édition.

Le 15 février 1982

Pierre Jaisson
Professeur à l'Université Paris XIII
Président de la Section française
de l'U.I.E.I.S.

PREFACIO

Durante el último congreso de la Unión Internacional para el Estudio de los Insectos Sociales (U.I.E.I.S.), que tuvo lugar en Wageningen (Holanda) en 1977, se manifestó el deseo de que la Union organizará la siguiente reunion internacional en un pais del Tercer Mundo y tratando sobre problemas que interesan más directamente a las zonas tropicales.

El primer simposio internacional «Los Insectos Sociales en el Trópico», cuyas actas estan reunidas en esta obra, fué la materialización de este deseo, fué también el primer coloquio internacional de esta especialidad que se efectua en el nuevo mundo. Pero fueron necesarios dos años de esfuerzos y la participación de numerosas personalidades y organizaciones científicas y culturales, para llegar a este resultado, à partir del momento en que me pareció que México era uno de los mejores lugares para acoger esta manifestación.

Desde el inicio del proyecto los estímulos del Dr. Raúl N. Ondarza, Secretario general de Comités del Consejo Nacional de Ciencia y Tecnologia (CONACYT) y del Dr. Gonzalo Halffter, Director del Instituto de Ecologia de México, me demostraron que existía efectivamente la posibilidad de organizar esta reunion científica en México. El interés y el apoyo del Dr. Edmundo Flores, Director general del CONACYT, permitieron lograr rapidemente la constitución de un Comité internacional y de un Comité local de Organización, habiendose originado este último de la Mesa Directiva de la Sociedad Mexicana de Entomologia (S.M.E.). La contribución del Dr. José Luis Carrillo, Presidente de la S.M.E., fué determinante como coordinador del Comité local, y también participó activamente en los trabajos realizados por el Comité internacional junto con los Drs. Raúl N. Ondarza y Dieter Enkerlin (México), los Professores Charles D. Michener, Presidente de la U.I.E.I.S. (E.U.) y Philip E. Howse, Secretario general de la U.I.E.I.S. (Inglaterra), quién desde el principio aportó su apoyo al proyecto. Todas estas personalidades tuvieron una participación activa, indispensable al éxito del simposio.

Pero nada de esto habría sido posible sin el apoyo material de Instituciones nacionales e internacionales. El apoyo del CONACYT fué determinante, por lo cual le manifestamos aqui el reconocimiento de la comunidad científica, así como a la Universidad Nacional Autónoma de México, al Instituto Politécnico Nacional, al Instituto Nacional de Investigaciones Agrícolas y al Colegio de Postgraduados de Chapingo, el cual organizó en esta ocasion un curso internacional sobre insectos sociales.

Agradecemos también el apoyo del Instituto de Ecología, del Centro de Investigaciones Ecológicas del Sureste y del Instituto Nacional de Investigaciones sobre Recursos Bióticos, así como a la UNESCO por la ayuda que nos aportó.

Fué gracias a todas esta instituciones que ha sido posible realizar la edicion de las Actas del Simposio, y también gracias a la colaboración del Centre National de la Recherche Scientifique (5e circonscription) y de la Université Paris XIII.

Obviamente es imposible traducir bajo esta forma toda la riqueza de las discusiones que se desarrollaron entre investigadores de 14 paises diferentes. Sin embargo, esperamos que estos dos volúmenes, que reunen 34 contribuciones repartidas por temas generales o por temas de especies (como en el caso de la mesa redonda organizada por el Professor Michener sobre la abeja africanizada), constituyan una referencia para los investigadores actuales y futuros interesados en los insectos sociales tropicales. Esta es la primera obra especializada, de carácter internacional, existente sobre el tema. Fué realizada sin ninguna finalidad lucrativa, lo que permitió fijar un precio de venta particularmente interesante. Los productos de la venta servirán para organizar otras reuniones científicas.

Terminaré este prefacio agradeciendo muy particularmente a los 51 especialistas, autores de los artículos incluidos en esta edición.

15 de febrero de 1982

Pierre Jaisson
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INTERSPECIFIC RELATIONSHIPS AND PREDATION

CHEMICAL DEFENCE IN TERMITES –
ECOLOGICAL ASPECTS

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SUMMARY

In a study carried out in the Federal District of Brazil, it was found that the defensive secretions produced by the nasute soldiers contain a variety of components, including monoterpenes. The monoterpenes were toxic on topical application to certain species of ant. Synthetic samples of these monoterpenes also acted as feeding repellents for the giant anteater. Soldiers with mechanical defence mechanisms rarely produce secretions which include the toxic secretions mentioned above. They appear to depend entirely on their powerful mandibles for colony defence. Species with defensive strategies based on chemical components produce large numbers of workers to feed them. This high investment in soldier production has resulted in a low investment in building activities and at the same a reduction in nest fortifications. The lack of a fortified nest is, however, compensated for by the toxic soldier secretions. The high soldier/worker ratio and the multidirectional action of the chemical secretions resulting from their volatility, allow the nasute species to forage on leaves and grasses on the soil surface. These food resources are rarely used in nest construction.

The corollary of this defensive strategy is found in species in which the soldiers have specialised in mechanical defence. These produce few soldiers and invest more energy

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in constructing nests more resistant to the attack of vertebrate predators. Such termites generally forage in galleries and feed on humus, depositing large quantities of soil which is used in constructing very resistant mound nests.

RESUMEN

Defensa quimica en los termites : aspectos ecologicos

En un estudio llevado a cabo en el Distrito Federal de Brasil, se encontró que las secreciones defensivas producidas por soldados nasutes contienen una amplia variedad de componentes, los cuales incluyen varios monoterpenos. Estos monoterpenos fueron tóxicos en aplicationes tópicas en ciertas especies de hormigas. Muestras producidas sintéticamente de éstos monoterpenos también actuaron como repelentes alimenticios del oso hormiguero. Los soldados de especies cuyos mecanismos de defensa son mecánicos, raramente producen secreciones que incluyen los compuestos tóxicos indicados anteriormente. Ellos parecen depender completamente de sus fuertes mandibulas para defensa de la colonia. Especies con estrategias defensivas basadas en compuestos quimicos, producen soldados de pequeño tamaño y en gran número y requieren por ello de un gran número de obreros para su alimentación. Esta alta inversion en la producción de soldados ha resultado en una baja inversión en actividades de construcción y al mismo tiempo en una reducción en la fortificación de sus nidos. La falta de un montículo fortificado es sin embargo compensada por los compuestos tóxicos en las secreciones de los soldados. La amplia relación soldado - obrero y la acción multidireccional de las secreciones quimicas debido a su volatilidad, permite a las especies nasutes de abastecerse con hojas y gramineas sobre la superficie del suelo. Estos recursos alimenticios son raramente utilizados en la construcción del montículo.

Lo opuesto a esta estrategia defensiva es encontrado en especies cuyos soldados se han especializado en defensas de tipo mecánico. Estas producen pocos soldados e invierten más energia en las actividades de construcción de montículos más resistentes al ataque de vertebrados depredadores. Estos termites generalmente se abastecen bajo protección y a menudo se alimentan en humus depositando grandes cantidades de suelo, el cual es usado en la construcción de monticulos de gran resistencia.

INTRODUCTION

Division of labour among different morphological castes is a marked characteristic of termite colonies. The soldiers are largely responsible for defence and have morphological adaptations for this function. Some species have soldiers with strong, thick mandibles specialised for mechanical defence whilst others have vestigial mandibles but produce complex defensive secretions. Although extensive literature on the chemical compositions of these secretions has become available in recent years (Prestwich, 1979) little is known of their action against natural predators or of their influence on other aspects of termite ecology. During three years fieldwork in the cerrado vegetation of central Brazil, observations were made on a series of termite species, their defensive strategies and ecology (Coles, 1980). In parallel with this fieldwork, chemical studies on soldier secretions were undertaken at Southampton University (Walmsley, 1981).

METHODS AND RESULTS

Chemical composition of soldier defence secretions

Soldiers and workers from 45 termite species were collected from excavated mounds and foraging parties. These were placed separately in vials of pure dichloromethane (Koch Light) and sent by air to Southampton University. Soldier-specific compounds were determined by analysing the volatile fraction of secretions using a variety of techniques including mass spectroscopy, gas chromatography and nuclear magnetic resonance spectroscopy (Walmsley, 1981). Several monoterpenes e.g. Limonene, phellandrenes, pinenes, were commonly found with diterpenes in the secretions of nasute species. Soldiers from species of the primitive genus *Syntermes* contain the monoterpene cis-ß-ocimene and various sesquiterpenes. *Armitermes euamignathus*, also in the Nasutitermitinae but with a well-developed nasus and mandibles, contained no terpenoid compounds but only the straight chain hydrocarbons tri-, tetra- and pentadecane. The majority of species with soldiers adapted for mechanical defence eg. *Orthognathotermes gibberorum, Termes bolivianus* and *Cavitermes parmae*, have no volatile soldier-specific compounds.

Biological action of defence secretions

Ant predators. A range of compounds was tested againts several species of ant common in the Distrito Federal. Small amounts of the synthetic compound being tested (0.15 μl/ant) were applied topically to the anterior dorsal thorax of each ant. Tests were carried out with 20 ants treated and 20

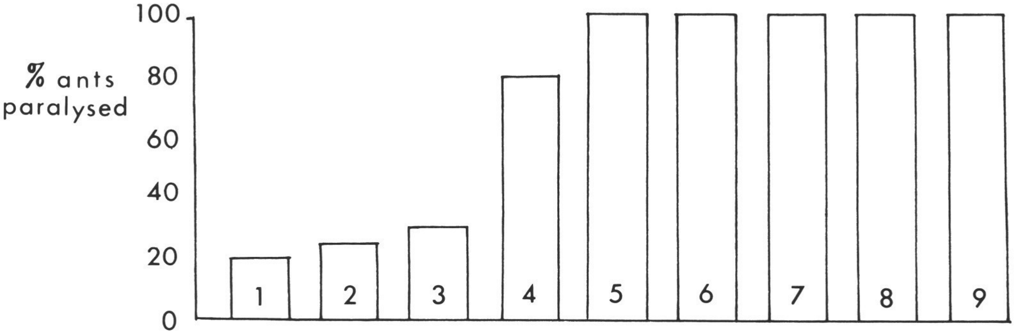

Fig. 1 – Maximum percentage of ants (*Camponotus* sp. A) paralysed by topical applications of test compounds (100 % conc., 0.15 μℓ/ant). Identification of the compounds tested is given below : 1 – n-pentadecane ; 2 – n-undecane ; 3 – myrcene ; 4 – β-pinene ; 5 – cis-β-ocimene ; 6 – α-thujene ; 7 – α-phellandrene ; 8 – α-pinene ; 9 – limonene.

Fig 1 – Porcentaje máximo de hormigas (*Camponotus* sp. A) paralizadas por aplicación tópica de compuestos probados (100 %) conc., 0.15 μℓ/hormiga). La identificación del compuesto probado esta marcada abajo.

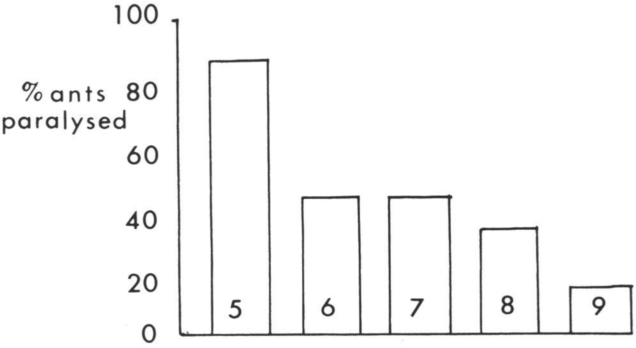

Fig. 2 – Time taken for five of the tested compounds to paralyse 100 % of the ants – *Camponotus* sp. A. (Topical application of 0.15 μℓ/ant to the dorsal, anterior thorax). Identification of the compounds is given below.

Fig. 2 – Tiempo necesario para que cinco de los compuestos probados paralizen 100 % de hormigas *Camponotus* sp. A. (aplicaciones tópicas de 0.15 μℓ/hormiga en el torax antero-dorsal). La identificación de los compuestos está marcada abajo.

as controls, in both open and closed petri dishes. The effects of the compounds tested varied both in severity and rapidity but in general produced paralysis and in some cases death. When death did not occur, paralysis lasted for several hours which would almost certainly lead to death under natural conditions due to predation and desiccation.

The varied effects of the compounds tested are shown in Fig. 1. The time taken to paralyse all the ants also varied and ranged from 16 minutes with 100 % concentrations of limonene and 92 minutes with cis-β-ocimene (Fig. 2). Dilutions of the most toxic monoterpenes were also tested. Ethanol, used as a solvent, was tested and shown to have no detectable toxic effect. Solutions of 80 % concentration had a more rapid toxic action than those of 100 % (Table 1). These differences are probably due to the solvent spreading the terpenes over the cuticle more effectively.

Mammalian predators. Food preference experiments were carried out using captive giant ant-eaters (*Myrmecophaga tridactyla*) and eight termite species representing different types of soldier defensive adaptations (Nasutes – *Nasutitermes* sp. n. D, *Cortaritermes silvestrii* and *Velocitermes paucipilis*, Mechanical – *Cornitermes* sp. n. A, *Procornitermes araujoi* and *Syntermes dirus* ; Soldierless – *Grigiotermes metoecus* ; Intermediate – *Armitermes euamignathus*). Tests were repeated on 8 days with different sequences of presentation of the termites (Coles, 1980, Coles de Negret and Howse, 1983). The results indicate that species with nasute soldiers are eaten less than soldierless species and those with soldiers specialised in mechanical defence.

Three synthetic monoterpenes, known to be present in nasute soldier defence secretions were tested as feeding deterrents. All three compounds were effective but varied in their degree of feeding inhibition. Limonene was the strongest deterrent followed by β-pinene and cis-β-ocimene in the approximate ratios of 11 : 1, 5 : 1 and 2 : 1 respectively.

Foraging strategies

A detailed study of the foraging behaviour of three species from the genus *Syntermes* was carried out near Brasilia. The foraging of *Syntermes* species is crepuscular and nocturnal. They form above-ground foraging parties and the termites are unprotected by soil sheeting. Data on the length of foraging trails, soldier to worker ratios and morphological adaptations of the soldier caste were collected. General observations were made on the feeding behaviour of a further 50 termite species from 29 genera found near Brasilia. The type and location of foraging (i.e. above ground, under soil sheeting, in

Table I – Effects of various monoterpenes applied topically to selected and species, including paralytic effects (PT$_{50}$) and recovery times, RT$_{50}$ (lethal effects).

Tabla I – Efectos de varios monoterpenes aplicados de manera tópica a varias especies de hormigas seleccionadas, incluyendo los efectos paralizantes (PT$_{50}$) y los efectos letales (RT$_{50}$).

Compound tested (0.15 µl/ant)	Conc. (%)	Ant species	Effect	PT$_{50}$ (min.)	RT$_{50}$ (min.)
(+)–limonene	100	A	+++	5.92	x
	80	A	+++	4.48	x
	60	A	++	11.95	1590
	40	A	+	–	
	20	A	0	–	
α-phellandrene	100	A	+++	13.65	>1000
	80	A	++	5.92	560
	60	A	+	8.23	12
	40	A	0	–	–
	20	A	0	–	–
	100	B	+++	9.57	–
	80	B	+++	10.16	–
	60	B	+++	12.64	–
	40	B	+	–	–
	20	B	0	–	–
(+)–α–pinene	100	A	+++	14.54	450
	80	A	+++	7.96	x
	80*	A	+	–	–
(–)–β–pinene	100	A	+++	11.85	220
	100	C	+	14.65	15–25
	100	D	++	38.25	90
α-thujene	100	A	+++	17.61	990
cis–β–ocimene	100	A	+++	–	–
n – undecane	100	A	+	–	–
n – pentadecane	100	A	+	–	–
	80	A	0	–	–
β–myrcene	100	A	+	–	–
Ethanol	100	A	0	–	–
	100	B	0	–	–

A : *Camponotus* sp. A
B : *Acromyrmex* sp. A
C : *Camponotus rufipes*
D : *Camponotus* sp. D

+++ : strong response
++ : medium response
+ : very weak response
0 : no difference from control response

x : no recovery apparent
– : not measureable
* : the lid of the petri dish was replaced with a gauze top in this experiment

the soil or in wood) was noted. Over 80 % of the above-ground foragers were found to have soldiers with monoterpenes in their defensive secretions. These same species have high soldier to worker ratios (Haverty, 1977, Redford & Coles de Negret, *in prep.*). Species with soldiers specialised in mechanical defence are generally restricted to foraging under the protection of soil sheeting or underground. These species have low soldier to worker ratios (Haverty, *op. cit.*, Redford and Coles de Negret, *op. cit.*).

The foraging strategies observed in the three *Syntermes* species reflect this general trend. *S. grandis* soldiers are adapted for mechanical defence and have a low frontal gland volume to head volume ratio. They produce no terpenoid compounds in their defence secretions (Baker et al., 1980), have a low soldier to worker ratio in foraging parties and form short above-ground foraging trails. *S. molestus* soldiers have a greater dependance on chemical defence with a relatively larger frontal gland volume to head volume ratio. They produce secretions rich in the monoterpene cis-β-ocimene (Baker et al., 1980), have high soldier to worker ratios in foraging parties and form long above-ground trails. *S. dirus* forms an intermediate between these two species.

Nest biology

Data on the mechanical resistance of termite mounds, the number of soldiers per unit time appearing at breaches, reconstruction activity by workers and numbers of inquiline termite species, were collected from a series of mounds (Coles, 1980). Termite species with nasute soldiers were found to build thin-walled fragile mounds which workers reconstruct slowly and with a high number of soldiers per unit time at breaches. Mounds of these species rarely have other inquiline termite species. Species with soldiers specialised in mechanical defence build thick-walled resistant mounds which workers reconstruct quickly but with a low number of soldiers per unit time at breaches. Multiple occupation of mounds of these species is very common and the inhabitants are protected then by both chemical and mechanical defence systems (Coles de Negret and Howse, 1983b, *in prep.*).

DISCUSSION

The defensive secretions produced by the nasute soldiers examined contain a variety of compounds including several monoterpenes which are toxic on topical application to certain ants. Synthetic samples of three of these monoterpenes were also shown to act as feeding deterrents to giant ant-eaters. Soldiers from species specialised in mechanical defence rarely produce secretions with these volatile toxic compounds. They appear to rely on large mandibles for defence.

The species *Armitermes euamignathus*, with soldiers specialised in both mechanical and chemical defence, presents an intermediate form of defence. Soldiers of this species produce no terpenoid compounds but straight-chain hydrocarbons which have little effect on topical application to ants. The mandibles alone are unlikely to provide an effective defence against potential predators. It is also doubtful that the slight toxic effects of the alkanes are enhanced by the cutting action of the mandibles because the hydrophobic nature of these compounds would allow them to penetrate the cuticular wax more quickly than body tissues. There remains the further possibility that the alkanes serve as «propaganda» pheromones against camponotine ants, common in the Distrito Federal, which produce similar compounds in their alarm pheromone. Ayre and Blum, 1971, and Blum, 1973, showed that camponotine ants produce un-, tri-, tetra- and pentadecane in alarm pheromones. Soldiers of *A. euamignathus* produce three of these alkanes in such large quantities (84 µg, 35 µg and 180 µg per soldier for tri-, tetra- and pentadecane respectively) that they may act as superpheromones disrupting the communication system of attacking ants thus reducing their potential as raiding predators.

The effects of different specialisations for defence in the soldier caste on the ecology of termite species is evident from the results presented above. Species with chemical defensive strategies produce many small soldiers and require a correspondingly high number of workers to feed them. This high investment in soldier production has resulted in a lower investment in building activities and reduced nest fortifications. The lack of a resistant mound is, however, compensated for by the toxic compounds in the soldier secretions. The high soldier to worker ratios and the multi-directional nature of the volatile secretions enables nasute species to forage above-ground for grass and leaves. This food source is rarely utilised in the construction of mounds. The corollary of this defence strategy is found in species with soldiers specialised in mechanical defence. These produce fewer soldiers and invest more heavily in building activities constructing mounds more resistant to attack by vertebrate predators. These termites generally forage under protection and often feed on humus, excreting large quantities of soil which is used to construct the hard mounds.

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FORAGING STRATEGIES AND THE STRUCTURE OF STINGLESS BEE COMMUNITIES IN COSTA RICA

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SUMMARY

The foraging behavior of *Trigona* (Apidae : Meliponinae) was observed in three habitats in Costa Rica. Eight foraging strategies were recognized in these eusocial bees, several of which could be employed by any given *Trigona* species. These were grouped into solitary foraging strategies and group foraging strategies.

In solitary foraging strategies, each bee makes its decisions to approach particular flowers, resin patches, mud holes, or other attractions independently of the decisions of its sister workers. Four solitary strategies were recognized. In *Avoidance*, a bee chooses not to forage near another bee or group of them, either to collect efficiently from a resource distributed as small units, or to avoid attack. In *Displacement*, a medium or large bee causes the departure of others from a resource by merely arriving or by arriving and behaving aggressively. In *Gleaning*, a small bee arrives at a flower after its peak of attractiveness or after other bees have exploited it, and collects leftovers. In *Insinuation* a small bee nervously but persistently collects from a resource defended by aggressive bees. In group foraging strategies, worker groups assemble at localized resources by means of communication and recruitment. Four group strategies were recognized. In *Scramble* group foraging the only effective competitive trait is the ability to recruit quickly to a locality ; that is, competition at the resource occurs principally by exploitation rather than by interference. In *Bustling* a group is recruited to a spread of resources, and other bees are discouraged from visiting by the hyperactive, «bustling» foraging movements of the recruits. In *Extirpation* a group is rapidly recruited to a resource and rivals are aggressively chased off. In *Opportunism*, a large colony usually forages as solitary individuals, but when an exceptional resource is found by one of the many searchers, they recruit quickly, and collect varying amounts of the resource while it persists, or until extirpators arrive and drive them off.

Illustrations of these foraging behaviors are given. Experiments reported for the first time include : 1/ *Trigona fulviventris* avoided landing on *Cassia biflora* flowers to which a dried, odor-free bee had been pinned. The speed with which the decision was made (seconds of hovering before landing or flying away) was significantly faster when the pinned bee was black (contrasting highly with the yellow flowers) than when it was orange (less contrasting). This suggests that the black color that typifies aggressive species may be an adaptation to permit swift recognition by timid species. 2/ Group foraging *Trigona fuscipennis* marked the *Wissadula* inflorescences they were visiting with visible droplets of mandibular gland pheromone. Incoming bees hovered beside these droplets before landing. When an unmarked, unvisited inflorescence was substituted for one of the marked, visited ones, the bees did not land on it. After these bees had been tricked into marking the unacceptable inflorescence, they landed on it regularly. This suggests that groups of *T. fuscipennis* arise because of mutual attraction to their own marking pheromone.

Stingless bees are generalists, and exhibit broad taxonomic overlap in the resources they visit. Their different foraging strategies, however, allow them to share resources by exploiting them at different times or different spatial densities. Although it is presumed the different foraging strategies evolved in particular resource and competitor environments, it is not known whether all combinations of foraging strategies are compatible and can co-occur in modern bee communities. Several ways of exoloring this question are described.

RESUMEN

Estrategias de forrajeo y estructura de las communidades de abejas sin aguijón de Costa Rica

El comportamiento de abastecimiento de *Trigona* (Apidae, Meliponinae) fué observado en tres localidades de Costa Rica. En estas abejas sociales, ocho estrategias de forrajeo fueron reconocidas, algunas puden emplearse para cualquier especie de *Trigona*. Hemos distinguido estrategias solitarias y estrategias colectivas de forrajeo. En las estrategias solitarias, cada abeja decide, independientemente de las decisiones tomadas por sus hermanas, si visita ciertas flores, manaderos alimenticios o pegotes de resina en los árboles. En la estrategia de *evitación*, una abeja decide que no forrajea cuando está próxima de otra abeja o grupo de abejas (con motivo de acumular eficientemente una fuente distribuida en cantidades pequeñas, o de no ser atacada). En la estrategia de *desplazamiento*, una abeja de tamaño mediano o grande causa la repartición de otras abejas en la fuente por el mero hecho de su llegada o por su comportamiento agresivo. En la estrategia de *espigueo*, una abeja pequeña visita una flor después de que ésta haya alcanzado su máximo de atracción, o recoge las sobras después de la visita de otras abejas. En la estrategia de *insinuación*, una abeja pequeña recoge, nervosa pero persistentemente, el néctar o polen de una fuente defendida por abejas agresivas.

En las estrategias colectivas de forrajeo, agrupaciones de abejas obreras se forman en los manaderos que han localizado por comunicación y reclutamiento. Quatro estrategias colectivas fueron reconocidas. En la estrategia de *arrebatiña*, la única característica efectiva y de competición es la habilidad de reclutar rapidamente para una localidad ; es decir que la competición en la fuente ocurre más por explotación que por intervención. En la estrategia de *agitatión*, un grupo de abejas se recluta a fuentes más dispersas y las otras se desaniman a visitar la fuente debido al movimiento agitado de las reclutadas. En la de *extirpación*, un grupo es rapidamente reclutado a un manadero y las abejas rivales son perseguidas con agresividad. En la de *oportunismo*, una colonia grande forrajea generalmente como individuos solitarios pero cuando una de las numerosas exploradoras en cuentra una fuente exceptional, se reclutan rapidamente y acumulan hasta que se acabe o que llegan las extirpadoras que las ahuyentan. Ilustraciones de estos comportamiento de forrajeo son dadas. Experimentos reportados por primera vez incluyen : 1/ *Trigona fulviventris* no se pone sobre flores de *Cassia biflora* donde una abeja seca e inodora ha sido pegada. La velocidad con la cual se decide a no posarse (segundos después de permanecer volando suspendidas) es significativamente más rápida cuando la abeja pegada es negra (contrastando con las flores amarillas) que cuando es de color naranjado (menos contraste). Esto sugiere que el color negro, que caracteriza las especies agresivas, es una adaptación que permite el reconocimiento rápido de las últimas por las especies tímidas. 2/ El grupo abastecedor, *Trigona fuscipennis*, marca (con gotas visibles de un olor producido por las glándulas mandibulares) las inflorescencias visitadas del género *Wissadula*. Las abejas que se acercan antes de posarse permanecen volando, suspendidas cerca de estas gotas. Cuando una inflorescencia que ha sido marcada es sustituida por otra que no lo había, las abejas no se ponen, hasta que la marquen de nuevo. Esto sugiere que los grupos de *T. fuscipennis* aparecen gracias a la atracción mutua que tienen para sus olores. Las abejas sin aguijón visitan muchas plantas de diversas clases y manifiestan un ámplio cruce taxonómico en las fuentes alimenticias que frecuentan. Sin embargo, las diferentes estrategias de forrajeo les permiten compartir las fuentes, explotándolas durante momentos distintos o segun las densidades. Aunque se supone que las diferentes estrategias de forrajeo se desarrollan en ambientes con fuentes particulares y de competición, no se sabe si todas las combinaciones de estrategias de forrajeo son compatibles y si podrían ocurrir también en comunidades de abejas modernas. Tres formas de examinar esta cuestión son descritas.

INTRODUCTION

In the eusocial insects natural selection shapes both the behavior of individuals and the emergent colony performance. In foraging, individual actions and group phenomena, mediated by communication and social facilitation, effect a distribution of workers in space and time, with consequences for foraging success. The patterns of worker allocation that are favored by natural selection depend on the dispersion of resource units (calories, for example) in space and time. Resources have a dispersion in and of themselves. In addition, other species or colonies, wherever they are better competitors, remove some kinds of resources from the available pool and leave others. Given diverse, yet limited resources, one would predict that in communities of social insects persisting over evolutionary time there would evolve a degree of complementarity of foraging strategies. I have documented complementarity of foraging strategies of *Trigona* bees (Apidae : Meliponinae) in three habitats in Costa Rica : the tropical dry forest of Guanacaste Province, the premontane wet forest at Turrialba, and the tropical wet forest of the Osa Peninsula. The *Trigona* in these sites have diverse, shared resources, and operate under conditions of at least intermittent food shortage (Johnson, 1974).

In the Costa Rican *Trigona* I studied I distinguished eight types of adaptive foraging strategies. Any given *Trigona* species could exhibit several of the strategies ; expression of the strategies depended on resource conditions, current forager deployment, and the nature of the competition. I will give the identifying features of each strategy, the types of species that use it, and how it works. I will conclude with a discussion of the extent to which one can expect *Trigona* species to be organized into communities of complementary foraging types. The eight strategies are grouped into four types of solitary foraging strategies and four types of group foraging strategies :

Solitary Foraging	Avoidance Displacement Gleaning Insinuation	Group Foraging	Scramble Bustling Extirpation Opportunism

In solitary strategies, each bee makes its decisions to approach particular flowers or resources independently of the decisions of its sister workers ; in group strategies, groups of foragers assemble at resources by means of communication and recruitment. Solitary and group deployment of foragers from a colony are contrasted diagrammatically in Figure 1.

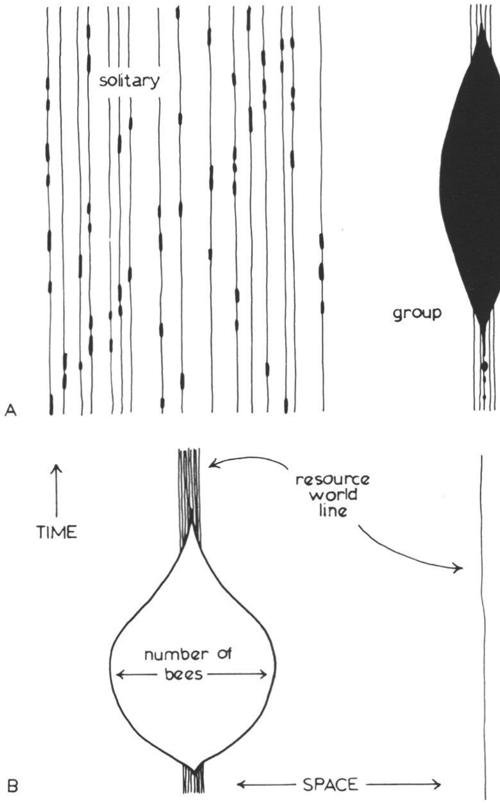

Fig. 1 – Graphical representation of the foraging of eusocial bees. A : Solitary and group foraging in space and time – B : the graphical conventions. Space is represented horizontally, time vertically. A plant resource is drawn as a vertical line or set of lines. The number of adjacent lines per resource indicates the relative richness of the resource in units such as calories, resin volume, or pollen grains. Bees at a resource are superimposed as a shape on the resource world line : width of the shape represents number of bees present at one time.

Fig. 1 – Representación gráfica del forrajeo de abejas eusociales. A : forrajeo solitario y colectivo en espacio y tiempo – B : las convenciones gráficas. Espacio es representado horizontalmente, tiempo verticalmente. El recurso de una planta es representado por una línea recta vertical o un grupo de líneas. El número de líneas adyacentes de cada recurso indica la riqueza relativa de los recursos por unidades como son calorías, volúmen de resina, o granos de polen. Abejas en un recurso son sobreiimpuestas como una figura en la línea «mundial» del recurso ; la anchura de la figura representa el número de abejas presentes en un momento.

SOLITARY FORAGING

Avoidance

In avoidance, a solitary forager chooses not to forage near another bee or group of them (fig. 2A). Why avoid ? Avoidance may improve foraging efficiency. Where the resource is distributed in small packets the sign of another bee on a packet indicates depletion. A suitable response would be to look for unoccupied flowers or resource sites. Avoidance may also prevent attack. Avoidance of this type can occur on a larger or richer resource, which is worth defending aggressively. Table I describes the circumstances under which one would expect to find avoidance as an efficiency mechanism and as an attack prevention device.

Table I – **Environments, in terms of resources and rivals, in which one would expect to find avoidance for efficiency and avoidance for attack prevention.**

Tabla I – **Los ambientes, en términos de recursos y competidores, en que se podía esperar encontrar evitación para el objeto de más eficiencia, y evitación para mejor prevención de ataque.**

	Environment				
	Resource		Bees avoided		
Function of avoidance	*Smaller, poorer*	*Larger, richer*	*From own nest*	*Poorer aggressive competitor*	*Better aggressive competitor*
Efficient foraging	+	–	+	+	+
Prevention of attack	+	++	–	–	+

As an example of avoidance I will report the results of an experiment that tested wheter *Trigona* could visually recognize competitors on flowers. I used *T. fulviventris* flying in to fresh *Cassia biflora* flowers in Guanacaste Province, Costa Rica, February, 1979. Hover time in seconds was recorded, and the subsequent action : land, leave, or touch down (defined as a landing too brief to be recorded on a stopwatch). Bees or models of bees could be pinned to a flower being watched. The bees were pinned specimens at least a year old from which all traces of pheromones and colony odors had presumably evaporated. As an added precaution the specimens were dried for another hour in an oven. The specimens used were of the same size as *T. fulviventris* and co-occured with them in Guanacaste ; they were *T. dorsalis*

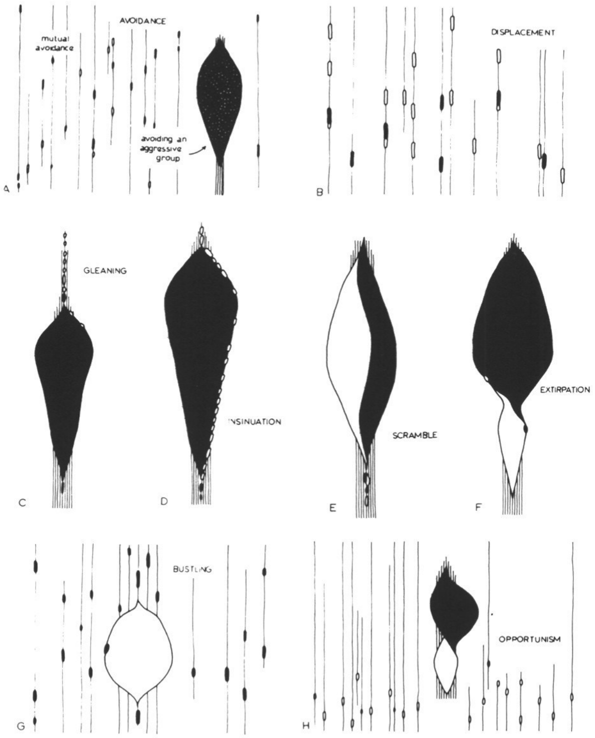

Fig. 2 – Hypothetical examples of the distribution of bees in eight types of foraging – A : AVOIDANCE. Two species of solitary forager (black ; white) avoid one another on the small resources, and both species avoid the aggressive group forager (hatched) on the richer resource – B : DISPLACEMENT. Three displacements are shown, in which an individual of one species (white) is replaced on the vertical track by an individual of another species (black) – C : GLEANING. Gleaners (white) visit a resource abandoned by a group foraging species – D : INSINUATION. Insinuators (white) feed beside aggressive bees (black) – F : EXTIRPATION. An extirpator species (black) chases off a less aggressive species – G : BUSTLING. A species using a bustling strategy (white) visits a patch of resource – H : OPPORTUNISM. An opportunist (white) during solitary foraging finds a rich resource soon after it comes into existence. The opportunist recruits and harvests until the extirpator (black) arrives.

Fig. 2 – Ejemplos hipotéticos de la distribución de abejas en ocho estrategias de forraje – A : EVITACION. Dos especies de abejas solitarias de forraje (negra ; blanca) se evitan mutuamente en los recursos pequeños ; y ambas especies evitan la especie agresiva que forrajea en grupos (rayado) en el recurso más rico – B : DESPLAZAMIENTO. Tres desplazamientos son ilustrados, en los que un individuo de una especie (blanca) es reemplazado en la rastra vertical por un individuo de otra especie (negra) – C : ESPIGUEO. Especies que espigan (blancas) visitan un recurso abandonado por una especie que forrajea en grupos – D : INSINUACION. Especies que insinuan (blancas) forrajean al lado de abejas agresivas (negras) – E : ARREBATINA. Dos especies o colonias reclutan al mismo recurso alimenticio – F : EXTIRPACION. Una especie extirpadora (negra) ahuyenta una especie menos agresiva – G : AGITACION. Una especie empleando una estrategia de agitación visita un área del recurso – H : OPORTUNISMO. Una abeja oportunista (blanca) mientras forrajea en solitario encuentra un recurso rico poco después de que êste aparece. La oportunista recluta y recolecta hasta la llegada de la extirpadora (negra).

(orange) and *T. fuscipennis* (black). The models were orange and black origami bees of equivalent size. The controls were the same flowers in the quarter hour after the pinned object was removed. No flower was used for more than one pinned object. The decision of *T. fulviventris* whether to land or leave was strongly influenced by the treatments (fig. 3). In the control situation *T. fulviventris* landed two out of three time (n = 30). Models reduced to tendency to land ($\chi^2 = 32.7$, $p < .001$) ; in addition, indecision appeared in the form of the brief landings called touch downs. When a flower contained a pinned bee, however, not once in 56 approaches did a *T. fulviventris* land. The distribution of responses differed from that for the controls ($\chi^2 = 111.9$, $p < .0001$) and from that for the models ($\chi^2 = 19.2$, $p < .0001$). These results indicate that *T. fulviventris* avoids *Cassia biflora* flowers that appear to be occupied, and that it can visually discriminate between real bee forms and surrogate bees. Further aspects of this experiment are described in the section on Extirpation.

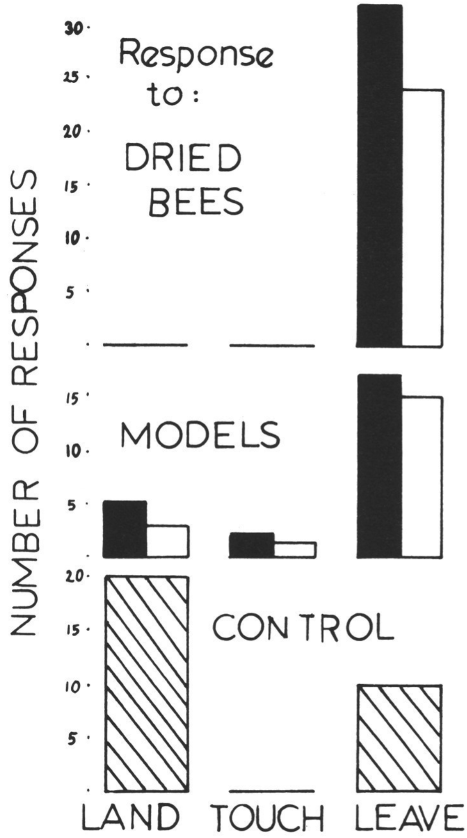

Fig. 3 – Frequency histogram of the responses by foraging *Trigona fulviventris* to control flowers and to flowers with a pinned bee or model. Responses to black bees or models are shown in black, responses to orange bees or models are shown in white, and responses to control flowers are hatched.

Fig. 3 – Una representación gráfica de la frecuencia de como responde *Trigona fulviventris* forrajeando a flores de control y a flores con una abeja prendida o con un lodelo de una abeja. Repuestas a abejas negras o a modelos negros son representados en color negro ; repuestas a abejas anaranjadas o a modelos anaranjados son representados en colo blanco ; y repuestas a flores de control son rayadas.

Generally, we would expect avoidance 1/ where the resource is unlikely to support two bees and where displacement of the first bee by the second is difficult, and 2/ on richer resources where an attempt to land might result in an annoying or damaging attack. We would expect species that commonly exhibit avoidance during foraging to be less aggresive in their physiological make-up, and more vulnerable than their opponents by virtue of smaller body size, weaker, duller mandibles, or other traits. *Trigona dorsalis* is one species that has been identified as an avoider (Johnson, 1974). For species intermediate in aggressive equipment we would expect decisions to avoid or not to avoid to occur after assessment of the rival, and to vary with the nature of the rival. For example, *T. fulviventris*, shown as an avoider, in other situations bites, attacks, or displaces weaker bees.

In summary, one would expect the selective environments favoring avoidance to be small, scattered, slowly-renewing or non-renewing resources, and bigger, sharper, meaner rival species.

Displacement

In displacement, an arriving individual causes the departure of one or more bees on a resource (fig. 2B). Large body size is the most salient charactertictic of a displacing species ; *Trigona capitata* and *Trigona silvestriana*, the largest of the *Trigona* with which I worked, were able to clear a «personal space» around themselves as they foraged. *Trigona capitata* is not only large, it has an unusually large head (for which the species, *capitata*, and its subgenus, Cephalotrigona, are named). The large head presumably enhances its ability to intimidate by cirtue of size, for Kikuchi (1965) reported a dominance hierarchy for flower-visiting insects based on head width. The head of *Trigona silvestriana* is not so large, but solitary foraging individuals will spice their displacement of rivals with a little aggression (Johnson, 1974 ; Hubbell and Johnson, 1978). Aggression may be more of an option for *T. silvestriana* than for *T. capitata* because *T. silvestriana* belongs to a subgenus with more mandibular teeth (Schwarz, 1948).

Examples of displacement, as well as avoidance, could be found in the visits by *Trigona fulviventris* and *T. dorsalis* to *Paspalum notatum* grass inflorescences in Guanacaste Province, Costa Rica, July, 1977. On July 22 I recorded the visitors every minute to 12 blooming plants (fig. 4). These data show four possible cases of interspecific displacement (on plants, H, H, S, T), and imply interspecific avoidance by the rarity of co-occurrence of the two bee species. The arrow points to the only time I recorded both *T. fulviventris* and *T. dorsalis* on the same plant. With the bee densities that morning, the probability of seeing one or fewer *T. fulviventris* co-occurring with *T. dorsalis* is $p < .002$.

Avoidance and displacement were confirmed by behavioral observations on July 21 in an adjacent 1 x 1.4 m plot with 12 blooming *Paspalum notatum*. The observational technique used was sequence sampling (Altmann, 1974).

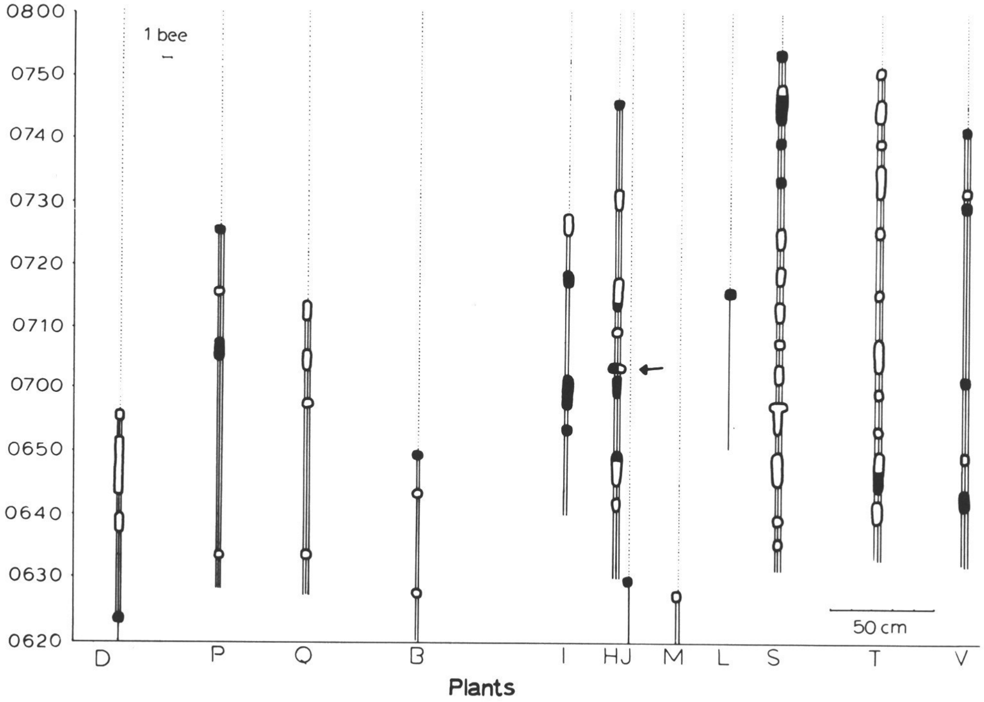

Fig. 4 – Visits by pollen-collecting *Trigona fulviventris* (white) and *T. dorsalis* (black) to 12 blooming grass plants (lettered). Approximate distance between plants is plotted on the abscissa. The vertical track for a plant starts at flower opening ; the number of lines in a track increases with the quality of the plant measured by the number of open flowers.

Fig. 4 – Visitas de *Trigona fulviventris* (blanca) y *T. dorsalis* (negra) a 12 plantas florecendas de hierba (con letras). La distancia aproximada entre las plantas es indicada en la abscisa. La rastra vertical de una planta empieza a la apertura de la flor ; el número de líneas en una rastra aumenta con la calidad de la planta medido por el número de flores abiertas.

A sequence began when an arriving bee hovered beside a bee on a plant, and ended when one or both left. All such interactive sequences involved either avoidance or displacement. An arriving bee was said to avoid if it flew in, hovered, and left, leaving the original bee on the plant. A bee on a plant was said to avoid if it flew away in response to an arriving bee that did not land. A bee on a plant was said to be displaced if it flew away in response to an arriving bee that did land. In the 5 interspecific encounters in which one bee avoided another, *T. dorsalis* always avoided *T. fulviventris*, hence I considered *T. fulviventris* dominant (Table II). In the 7 interspecific encounters in which one bee displaced another, *T. fulviventris* always did the displacing, so again I considered *T. fulviventris* dominant. In this case the displacer, *T. fulviventris*, is the same size as the avoider, *T. dorsalis*. This study accords with years of observation that for whatever reason of internal construction *T. fulviventris* is a more aggressive insect than *T. dorsalis.*

Table II – Interactions of *Trigona fulviventris* (F) and *T. dorsalis* (D) at grass inflorescences. All interactions ended in avoidance or displacement of one bee by another. A binomial test rejected the null hypothesis that F and D are equally likely to win an encounter.

Tabla II – Acciones reciprocas de *Trigona fulviventris* (F) y *T. dorsalis* (D) a inflorescencias de hierba. Todas las acciones reciprocas terminaron en evitación o desplazamiento de una abeja por otra. Una prueba de binómino negó la hipótesis nula que F y D tengan la misma probabilidad de ganar.

	Avoidance		Displacement		Both		
	Loser		Loser		Loser		
Winner	F	D	F	D	F	D	
F	3	5	2	7	5	12	
D	0	2	0	0	0	2	
	p =. 625,		p =.0156,		p =.00049,		two-tailed

The selective resource environments that would favor displacement include resources that can support several visits. Such resources may either have room for about one bee, or be bigger, with sufficiently simple topography that the displacer can easily see rivals on them. The competitor environments favoring displacement are smaller or weaker rivals with poor recruitment capability.

Gleaning

Among solitary foragers, avoidance and displacement result primarily in spatial separation. Gleaning, on the other hand, is a form of temporal avoidance. A gleaner arrives at a flower after its attractiveness has peaked and harvests the leftovers (fig. 2C). For the amount of leftovers to be worth the visit, one would predict the gleaner to be a tiny insect relative to the flower. The bee I have found to be a gleaner is *Trigona buyssoni*, which at 2.5 mm is about as tiny as stingless bees come (Schwarz, 1948). Solitary foragers of *T. buyssoni* collected scattered pollen from *Ardisia revoluta* in Guanacaste, Costa Rica, until at least 1100 hours, even though *Ardisia* flowers peaked in fragrance and attractiveness to bees at 0700 (1.2 bees/inflorescence) and were wilting and largely abandoned by bees at 0900 (0.04 bees/inflorescence).

Wille (1963) used the term «gleaning» in a slightly different sense to describe foraging in *Trigona*. Wille's gleaners were small to medium *Trigona* that visited *Cassia biflora* flowers after the tubular anthers enclosing the pollen had been buzzed or bitten into by larger, stronger bees. These smaller bees than picked up loose pollen grains left on the corolla and anthers. In gleaning in Wille's sense, the priority of larger bees is necessary because it is they that convert the resource into a state that is usable by the smaller bees. Gleaning, in the sense intended here, has the smaller bees arriving later to avoid interference competition from bigger rivals. Since flowers with accessible pollen predominate in the tropics (Wille, 1963), I predict one will find most cases of pollen gleaning to be an adaptive response to interspecific competition. The extent, significance, and dynamics of gleaning, however, remain largely to be demonstrated. Environments favoring the evolution of gleaners would contain ample, clumped resources not always neatly extracted, that attract larger, stronger, solitary or group-foraging competitors.

Insinuation

Wilson (1971) described «insinuator» ants that «... rely on small size... and lack a soldier caste». They do not recruit many workers and «... are usually able to ease their way to the edge of sugar baits through crowds of «extirpator» workers without eliciting aggressive responses».

Like Wilson's ants, *Trigona* insinuators are small and unaggressive and will feed among a crowd of aggressive group foragers (fig. 2D). Insinuator species include *T. latitarsis, T. testaceicornis, T. frontalis, T. buyssoni*, and *T. jaty* (Johnson, 1964 ; Johnson and Hubbell, 1974 ; Hubbell and Johnson, 1978 ; J. Howard, pers. comm.). These species have relatively small colony sizes and recruit poorly. They fly off or back away when threatened, but are persistent and soon land nearby.

If insinuators are small, and few in number because they recruit poorly, but are persistent, the energy and aggressor would expend to keep them at bay could well exceed the calories the aggressor would lose to them if unmolested. The strategy selected for in the aggressor would be to attack only rarely- -just enough to hold down any evolutionary tendencies to exploit the aggressor's resources more fully.

The effectiveness of insinuation can be seen in the relative success of the small, persistent insinuator *T. testaceicornis* and the medium-sized non-insinuating *T. fulviventris* visiting sugarwater baits alongside the large, aggressive *T. silvestriana*. Hubbell and Johnson (1978) monitored a grid of 38 baits for 10 census periods, encompassing an area that contained 4 nests of *T. testaceicornis* and 1 nest each of the other two species. In only 9 cases did

T. fulviventris and *T. silvestriana* co-occur on a bait, and in the majority of these cases, joint occupancy meant just one bee of each species. A pairwise test of association for presence or absence showed negative association ($p < .00001$). In contrast, *T. testaceicornis* insinuated itself onto baits sometimes occupied by more than 20 *T. silvestriana*, and co-occured with them in 70 cases. The association is negative, but much less so ($p < .001$).

A second look at insinuation is provided by three species of *Trigona* visiting a resin source. The bees were collecting from wounded stems of *Macherium kegelii*, a papilionoid legume vine, in Guanacaste Province, Costa Rica, July, 1977. Figure 5 shows the numbers of each species over time sitting on the resource, and hovering above it. At 0741 hours at least 7 aggressive *T. silvestriana* recruits arrived in a group and took over the resin source. *Trigona dorsalis* and *T. frontalis* present in approximately equal numbers in the 10 min before the takeover, responded to the takeover with shorter individual landing times and fewer bees landed per census. The two species

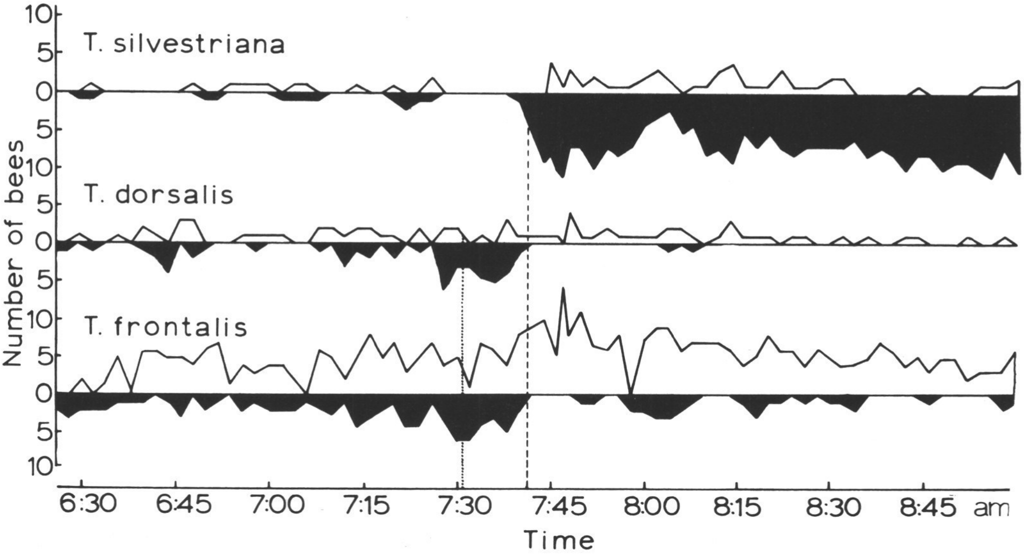

Fig. 5 – Bees at a resin source. Lower graphs (black) show the number of settled bees ; upper graphs (white) show the nomber of bees hovering in a defined zone above the resin. From 0731 to 0741 (between the dotted and dashed lines) approximately equal numbers of *Trigona dorsalis* and *T. frontalis* settled. At 0741 (dashed line) *T. silvestriana* arrived.

Fig. 5 – Abejas en una fuente de resina. Las representaciones gráficas más bajas (negras) muestran el número de abejas asentadas ; las más elevadas (blancas) muestran el número de abejas que se cernan en el aire en una zona definida sobre la resina. De las 0731 a 0741 horas (entre las líneas de puntos o de guiones), approximadamente números iguales de *Trigona dorsalis* y *T. frontalis* se asentaban: A las 0741 horas (linea de guiones), *T. silvestriana* llegó.

differed in their foraging success in the ensuing hour, however. Two *T. dorsalis* landed after the first burst of *T. silvestriana* recruits returned to the nest with their harvest, but no further landings for *T. dorsalis* were recorded in the subsequent hour. The number of hovering *T. dorsalis* dwindled to approximately one. In this way the medium-sized *T. dorsalis* behaved as an avoider. In contrast, the tiny insinuator *T. frontalis* accomplished 14 times as many visits, and was still present at the end of the hour, both hovering over the resin source and collecting from it. Figure 5 shows that while it is more profitable for an insinuator such as *T. frontalis* to have the resource to itself, harvest is still possible in the presence of an extirpator.

GROUP FORAGING

Scramble

Group foraging in stingless bees involves recruitment to particular locations, often by means of pheromones (Kerr, 1969). As with other eusocial insects (von Frisch, 1967 ; Wilson, 1971) the resources to which *Trigona* recruit are rich and ample enough to be worth the efforts of additional bees. In scramble group foraging the only effective competitive trait is the ability to recruit quickly and well to a small region of interest. If a similar colony recruits to the same resource, both scramble for it, neither denying the other access (fig. 2E). In other words, exploitation rather than interference competition is observed (Miller, 1967).

Scrambling foraging was observed in *Trigona testacea* and *T. mexicana* collecting pollen from adjacent *Bactris* inflorescences in Turrialba, Cartago Province, Costa Rica, July 21, 1971 (fig. 6). Through some combination of recruitment or learned experience with the opening time of *Bactris*, the two species built up their numbers and swarmed over the flowers. It was hard to tell if the occasional dislodged bee was attacked or simply jostled ; in any case, neither species prevented the other from exploiting the flowers.

On the following day I set up an analogous situation on the ground in order to observe whether these two medium-sized species attacked one another (interference competition) or whether their attention was directed entirely to the resource (exploitation competition). Randomly selected bees were followed through one feeding visit to a 0.8 M sucrose bait erected near the *Bactris*. Behaviors and their duration were recorded in sequence with a battery-powered event recorder, beginning with «hover» and ending with «fly away». In the 293 seconds that comprised the totaled visits of 8 *T. testacea* and 10 *T. mexicana*, there were 4 acts of interspecific aggression :

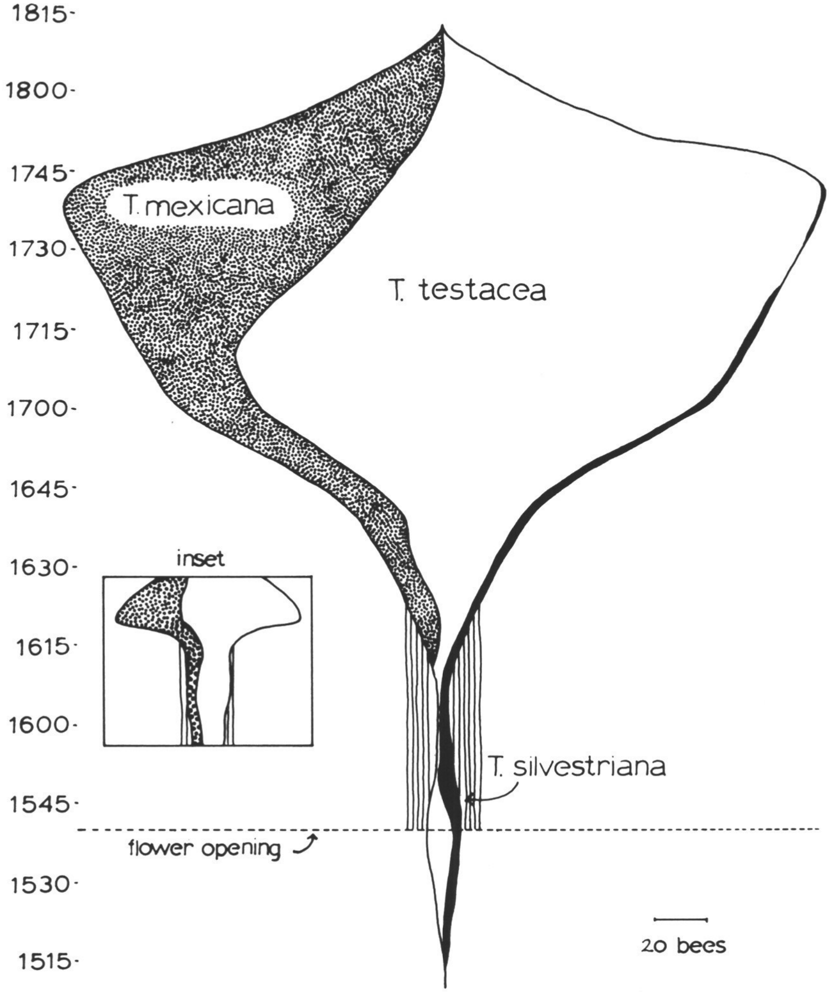

Fig. 6 – The numbers of *Trigona silvestriana* (black), *T. testacea* (white), and *T. mexicana* (stippled) visiting a pair of *Bactris* palm inflorescences 30 cm apart at their bases. The decline in bee numbers coincided with dusk. INSET : visits by *T. testacea* and *T. mexicana* to a sugarwater food dish 20 m from the tree. The inset is drawn to the same scale as the figure, but spans the time from 1255 to 1332 hours.

Fig. 6 – Kis números de *Trigona silvestriana* (negra), *T. testacea* (blanca), y *T. mexicana* (punteada) visitando un par de inflorescencias de la palma *Bactris*, las bases de éstas apartadas 30 cm. La reducción en el número de abejas coincidió con el crepusculo. GRAFICA INTERTADA : visitas de *T. testacea* y *T. mexicana* a uno plato con alimento (solución de azucar en agua) a 20 m del árbol. La representación gráfica insertada es dibujada a la misma escala que la figura, pero abarcando el tiempo desde las 1255 à 1332 horas.

3 threats and 1 attack (i.e., T_1 chased M_1, M_2 opened its mandibles at T_2, M_3 leaned at T_3, and M_4 seized T_4 for 2 seconds). Only in the case of seizure did the aggressor cause departure from the resource. Despite these sporadic incidents both species exploited the resource heavily (fig. 6, inset).

Although the two scramble group foragers did not exclude one another, they did create a situation in which the strategies of other *Trigona* fared poorly. None of a handful of hovering insinuators managed to land between 1700 and 1810. When an inflorescence swarms with 5-6 mm bees, there are few safe corners in which tiny insinuators can land, even briefly. The displacement strategy of *T. silvestriana* was likewise ineffective. At first *T. silvestriana* matched *T. testacea* in numbers (fig. 6), and delivered threat displays to insinuators, wasps, *T. testacea*, and *T. mexicana*, which were acknowledged by flight and other forms of retreat. After 1640, however, such displays went unnoticed in the confusion, and visits by *T. silvestriana* descreased. Although *T. silvestriana* can recruit and be an effective extirpator (Johnson and Hubbell, 1974 ; Johnson, 1981), it is not as «cohesive» in space and time as some group foragers, and thus comes to be competitively outnumbered in certain situations (Johnson, 1974 ; Hubbell and Johnson, 1978). Once *T. silvestriana* is outnumbered by a scrambling mass of bees, there may be the additional difficulty of «tracking» individuals for a biting attack. A filmed study of *T. silvestriana* under varying conditions of competitive crowgind would be instructive.

Scrambling might be expected to evolve in sturdy bees with large colonies in environments with large, rich, but transient resources. Bees preadapted for scramble group foraging would probably not include bees specialized for aggression, which would be so aroused by crowds of rivals that they could not concentrate on simple resource exploitation.

Bustling

Bustling is like scramble in that recruited groups forage on ample resources without attacking other bees. Yet the bustling strategy has certain peculiarities. Since I have found this strategy only in *Trigona pectoralis* Dalla Torre, I will describe some features of the foraging of *T. pectoralis*. Of the species I compared in one patch of tropical dry forest in Guanacaste, Costa Rica, *T. pectoralis* was most often found in large groups (defined as 10 or more) ; about 80 % of the time I saw any, I saw many (Johnson, 1974). A group, however, was not highly localized in space as it would be if scramble group foraging were occuring ; rather, the group was spread out over much of the extent of whatever flower species they were visiting. This suggests that pheromone marking of food sources, if any, may be diffuse. A preliminary analysis of the area extent and caloric dispersion of the subset of floral resources visited by *T. pectoralis* suggests they visit mainly resources that can provide for many bees at once, resources such as *Byrsonima*, a tree, *Cochlospermum*, also a tree, and *Mimosa pudica*, a cesalpinaceous herb which covers large areas with small flowers (Johnson, unpubl.). A *T. pectoralis* colony, moreover, tends to forage as a unit, which results in a lower daily pollen diversity than that of a solitary foraging colony. For example, Klahn (unpubl.) sampled pollen loads every morning for 3 months at colonies of two species, the group forager, *T. pectoralis*, and a predominantly solitary forager, *T. fulviventris*. The pollen diversity for *T. pectoralis* during three morning hours was 3.36 ± 0.24, whereas that of *T. fulviventris* was 7.78 ± 0.40. These differences are significant ($p < .0001$). Additional day-long sampling showed that the 3 to 4 species *T. pectoralis* collected in the morning hours represented the plateau level of diversity for the day, whereas the total daily pollen diversity of *T. fulviventris* was close to 20.

What is interesting about *T. pectoralis* is that whereas it is unaggressive as it forages, at least a third of the time one finds it in monospecific groups (Johnson, 1974), which arise in part because other bees get out of the way of this middle-sized *Trigona*. I speculate this has to do with the way individual *T. pectoralis* move as they forage. An individual forages in a hyperactive manner, stopping only briefly. Such bustling activity may be an adaptation to collect all the tree or patch has to offer during the time available. Because forward movement directed at another bee is a component of threat behavior in other *Trigona*, some movements of *T. pectoralis* may appear to a competitor to be in its direction. As the *T. pectoralis* themselves are accustomed to such activity, it perturbs them little, and several colonies may forage together (Johnson, 1974), a situation not observed for aggressive group foragers.

The proposed bustling strategy (fig. 2G), like scramble group foraging, would be used on a resource that could support many bees. The difference would be that the resource would be spread over a considerable area, and recruitment would be less localized.

Extirpation

Extirpation, to use Wilson's (1971) colorful term, is a group foraging strategy in which bees are recruited massively to a place, and any rivals encountered are chased off (fig. 2F). The localized resource must, of course, be ample enough to supply the aggressive group. In fact, the resources which extirpators frequent are both calorically rich and spatially compact (Johnson, 1974). By means of sugarwater baiting experiments it was determined that both richness and spatial clumping are important to the extirpator strategy.

In an experiment testing the effect of sucrose concentration on the expression of aggression Johson and Hubbell (1974) offered baits of 5 sucrose concentrations in a 5 x 5 array. Three colonies of the extirpator *Trigona corvina* Cockerell fought over the baits. The intensity of fighting, measured by the number of fights and deaths associated with each concentration, increased with molar concentration. This result implies that extirpators are more willing to incur the costs of aggression when the rewards to be won are large.

Johnson (1981) later tested the effects of spatial dispersion of a resource on its defensibility by an extirpator. The baits were hung from clotheslines and could be arranged singly, or pushed together in clumps of ten. The defense of the baits by *T. silvestriana* against *T. corvina* was 20-30 times more successful when the baits were grouped than when they were regularly spaced. Because rich resources are more valuable and more defendable, one could propose that extirpation was selected for in environments containing just such large, rich resources. It also seems reasonable that aggressive group foragers would have physical traits that enhance their aggressive success. Such traits could either evolve in species using aggressive tactics, or could be preadaptations facilitating the evolution of aggressive behavior. Success-enhancing traits of extirpators include medium to large body size, toothy mandibles, black color, and dark wings. Extirpators use these traits in threat displays (raising up on the legs, opening the mandibles, and sticking the wings out), and may follow up the threat with a biting attack (Johnson and Hubbell, 1974 ; Roubik, 1980). Medium to large body size and well-developed mandibular teeth are of obvious importance, and occur in all New World extirpators so far designated. Dark bodies and wings, in turn, may make a displaying bee more conspicuous against a bright background ; black color characterizes the extirpators *T. fuscipennis, T. silvestriana, T. corvina, T. hyalinata branneri*, and *T. amalthea*, but not the orange extirpators *T. pallens pallens* and *T. williana* Schwarz, 1932 ; Wille, 1965 ; Johnson and Hubbell, 1974 ; Hubbell and Johnson, 1978 ; Roubik, 1980 ; Johnson, 1981). Extirpators also recruit quickly to a point in space (fig. 10). Sometimes the first recruits arrive in a well-defined group (Hubbell and Johnson, 1978 ; Roubik, pers. comm.), which makes takeover swifter and surer. To accomodate such recruitment, the colony size of extirpators is large and the entrance is wide.

Recently I tested the hypothesis that black color is an adaptation of aggressive species which renders them more salient to timid species. In the section on Avoidance I described an experiment in which *T. fulviventris* flew to control *Cassia* flowers or to flowers with pinned bees or models. The bees usually chose to land on the control flowers, usually chose to fly away from the flowers with models or live conspecifics, and always chose to fly away from flowers with pinned bees (fig. 3). Figure 7 shows the frequency histograms of the number of seconds of hovering until these decisions were made. Decisions were made quickly in the control situation ($x = 1.8$ sec) and when a live conspecific was on the flower ($x = 1.8$ sec). Significantly longer times compared to the controls were required to reach a decision about the model ($x = 3.2$, $p < .01$, 2-tailed, Mann-Whitney U). The most dramatic contrast, however, was between the pinned orange bees and pinned black bees. Although the decision in both circumstances was invariably to leave, the decision was reached about three times as fast when the pinned bee was black ($x = 1.6$ sec) than when it was orange ($x = 4.4$ sec, $p < .001$, 2-tailed, Mann-Whitney U). I interpret this to mean that black, contrasting color permits almost instant recognition of characteristic bee form whereas orange color does not.

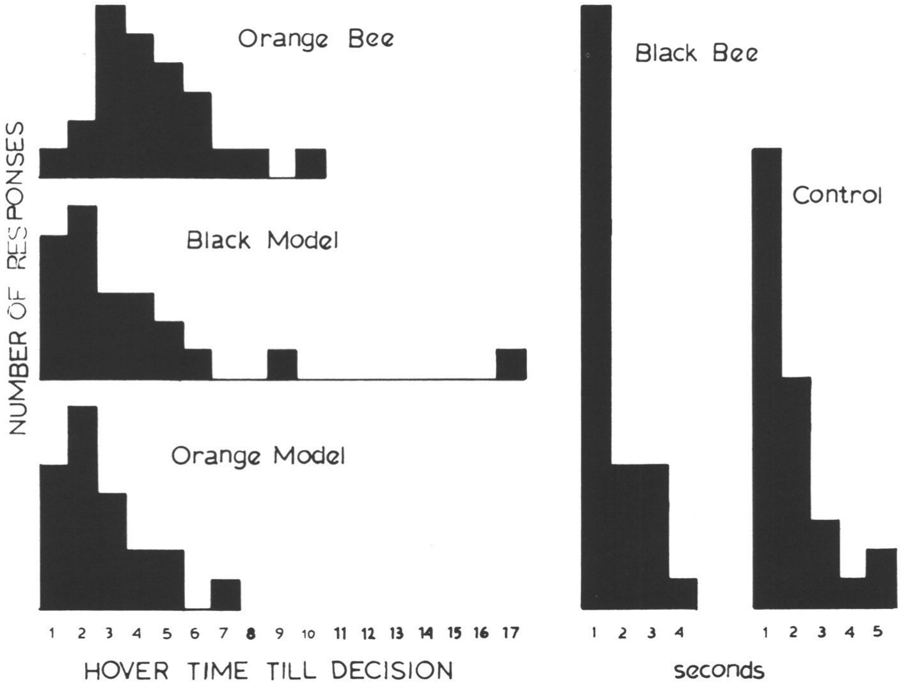

Fig. 7 – Seconds of hovering before decision to land, leave, or touch down was made by *Trigona fulviventris* flying to control *Cassia* flowers, or to flowers containing pinned orange or black bees or bee models. Each square of the frequency histograms represents the hover time of one bee.

Fig. 7 – Segundos de cernerse en el aire antes de la decisión de aterrizar, de marcherse, o deposarse fué hecho por *Trigona fulviventris* volando a flores de *Cassia* de control, o a flores conteniendo abejas prendidas, anaranjadas or negras, o modelos de abejas. Cada cuadrado en las columnas de la frequencias representa el tiempo de cernerse en el aire de una abeja.

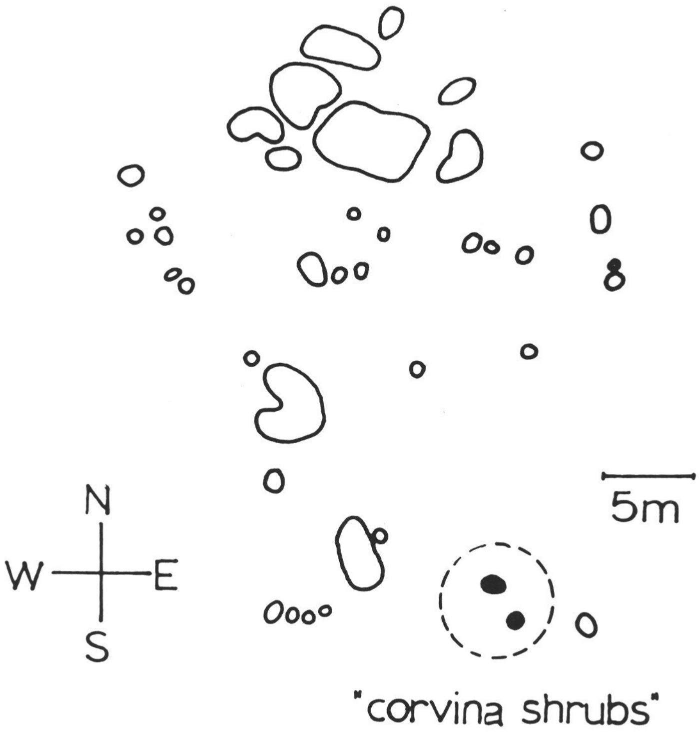

Fig 8 – *Cordia inermis* shrubs on savanna, Guanacaste, Costa Rica. Nineteen of these shrubs had open flowers on August 24 and 25, 1973. In three censuses, 135 *Trigona corvina* were counted, all but one of them on the two shrubs they monopolized (black). On the other 17 flowering shrubs I counted 804 *T. pectoralis, T. fulviventris, T. frontalis*, and *T. testaceicornis*.

Fig. 8 – Arbusto de *Cordia inermis* en sabana, Guanacaste, Costa Rica. Diez y nueve de estos arbustos tuvieron flores abiertas el 24 y 25 agosto, 1973. en 3 censos 135 *Trigona corvina* fueron contadas pero todas menos una de ellas estaban localizadas solamente en dos plantas, las que monopolizaban completamente (negras). En lo demás 17 de los arbustos, conté 804 *T. pectarolis, T. fulviventris, T. frontalis*, y *T. testaceinornis.*

The most extreme extirpators are black, medium-sized species with large colony sizes, namely, *Trigona corvina* and *T. fuscipennis*. These bees cluster in tight monopolistic groups on resources. If the resource is spread out, instead of covering it as the bustling *T. pectoralis* would, the extreme group foragers cluster on one part of it (fig. 8). The basis of such clustering appears to be the strong attraction of these extirpators to their own marking pheromone. Such attraction was shown experimentally in a group of *T. fuscipennis* visiting dried *Wissadula* inflorescences in Guanacaste Province, Costa Rica.

Although these malvaceous forbs were spread over a 150 m^2 area, the *T. fuscipennis* chose to visit only 4 unremarkable adjacent specimens. The bees flew in to the plants with a speed and directness that suggested visual orientation, hovered a few seconds, and landed. They also marked the 4 plants with discernible pheromone droplets from their mandibular glands. It was beside these droplets that incoming bees did their hovering. In a control experiment I counted all bees that hovered and landed on a selected inflorescence during a 15 min period. In all 25 bees hovered of which 21 landed (Table III).

Table III – Response of *Trigona fuscipennis* foragers to *Wissadula* stalks, marked and unmarked with pheromone, at the site of the original, marked stalk.

Tabla III – Repuesta de abejas de *Trigona fuscipennis* a inflorescencias secas de *Wissadula*, marcada o no marcada con perfume, en el sitio de la inflorescencia original.

	#of bees that hovered	#that landed	percent of hoverers that landed
original, marked stalk	25	21	84 %
transplanted, unmarked stalk	17	0	0 %
both stalks, tied together	21	14	67 %
transplanted stalk, now marked	13	9	69 %

Then I cut the stalk and replaced it with an unvisited one of the same length and number of dried flowers. In 15 min 17 hovered and none landed. In each case the bee approached rapidly, as before, began to hover, then suddenly backed up 80 cm or more, flew rapidly up and down the inflorescence, and took off. At least 9 of these bees then flew up and down one of the three adjacent visited inflorescences, damped their amplitude within 4 sec to a stationary hover, landed, and foraged.

Next I took the original inflorescence and tied it to the transplanted inflorescence so that the two were juxtaposed. The droplets had not been replenished since the control experiment. Even so, in the next 15 min 21 bees hovered of which 14 landed on the tied stalks. Some of them visited and marked the transplanted stalk. Finally I removed the original inflorescence. This time the bees did land on the now marked, transplanted inflorescence ; in 15 min 13 hovered of which 9 landed. The hovering time was the usual 2 to 5 sec and the bees did not fly up and down the stalk. I conclude that attraction to their own marking pheromone can explain the tight foraging clusters of extreme group foragers. The small area covered by a dense group of extirpators makes it possible for them to exclude outsiders and monopolize the area they visit. Such tight formations of the medium-sized black bees can be contrasted with the looser groups of the larger *T. silvestriana*, a displacer/

extirpator. Hubbell and Johnson (1978) computed species diversity indices for 114 sugarwater baits set out in the dry forest over two days of census intervals. The least diverse baits were those occupied by the extirpators *T. silvestriana* and *T. fuscipennis*, but the baits of *T. fuscipennis* were considerably less diverse according to Brillouin's index (0 - .1) than those of *T. silvestriana* (.2 - .3).

Environments that would select for extirpation strategies would likely be ones in which there is intense intraspecific competition for successful acquisition of compact but ample resources of sufficient rarity so as to be limiting.

Opportunism

Consideration of the last foraging strategy, opportunism, brings us up against a major drawback of the extirpator strategy. Extirpator bees, normally clumped offensively or defensively in space (Johnson, 1974), are not scattered all over the landscape finding new resources. It is opportunistic species with large colony sizes foraging solitarily most of the time that find good new resources first. In dozens of experiments it has been the aggressive group forager or extirpator that was the last to find new sucrose baits, and the opportunist that was the first (Johnson, 1974 ; Hubbell and Johnson, 1978). An opportunist is a species with many foragers searching independently in the field. When one of them finds an exceptional resource it can quickly recruit, drawing the far-flung net of bees into one spot for harvest. When – or if – an extirpator finally arrives, the opportunist rarely stays to fight. The advantage of the opportunist has been to be early (fig. 2H). I have found one species with this strategy, *Trigona fulviventris*, a normally solitary forager (Johnson and Hubbell, 1975) with up to 2000 bees out in the field at a time (Johnson, unpubl.), capable of swift recruitment to a location (Johnson, 1980).

Figure 9 shows the stages of occupancy of a grid of sugarwater baits visited by the opportunist, *T. fulviventris*, and an extirpator, *T. silvestriana*. *T. fulviventris* discovered the baits in half an hour, recruited, and spread out from the point of discovery. *T. silvestriana* did not discover the baits for five and a half hours. It then recruited, spread out from its center of discovery, and pushed *T. fulviventris* to the periphery of the grid. As *T. silvestriana* spread from its different discovery point it found baits that had already been found by *T. fulviventris* more frequently than could be explained by chance (a binomial test rejected the null hypothesis that the P values, giving the p of k or more successes in a given census period, are uniformly distributed ; p = .0112). This raises the interesting possibility that *T. silvestriana* may be exploiting the ability of *T. fulviventris* to find new resources readily.

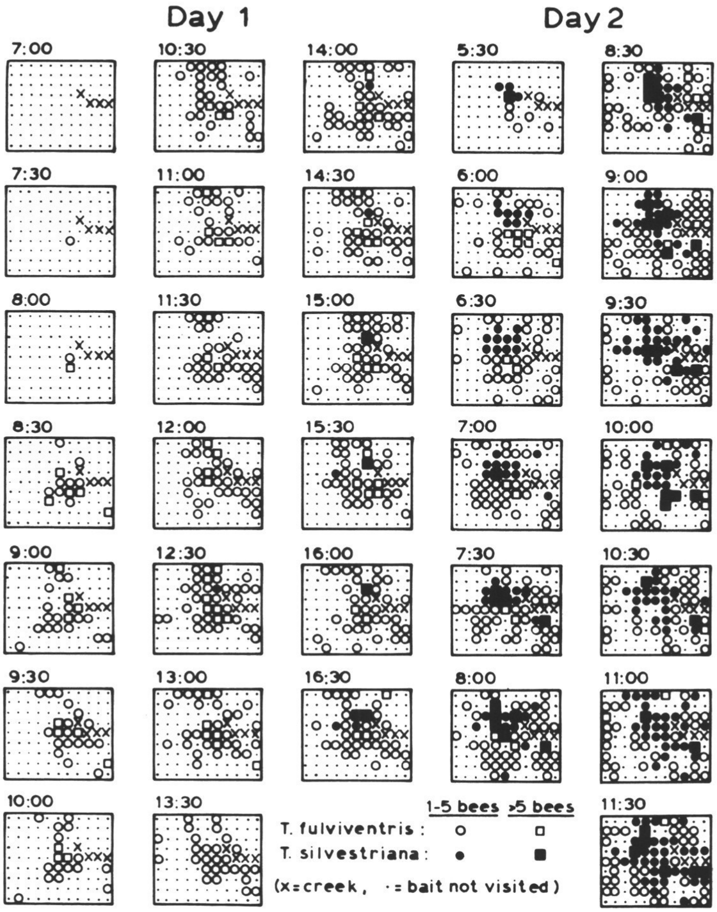

Fig. 9 – Visits by *Trigona fulviventris* and *T. silvestriana* to a 160 x 200 m grid of baits in a tropical dry forest, Guanacaste Province, Costa Rica, July 30-31, 1977.

Fig. 9 – Visitas de *Trigona fulviventris* y *T. silvestriana* a una rejilla de 160 x 200 m con cebos conteniendo un solución de azúcar en agua en un bosque seco tropical, en la Provincia de Guanacaste, Costa Rica, 30-31 julio, 1977.

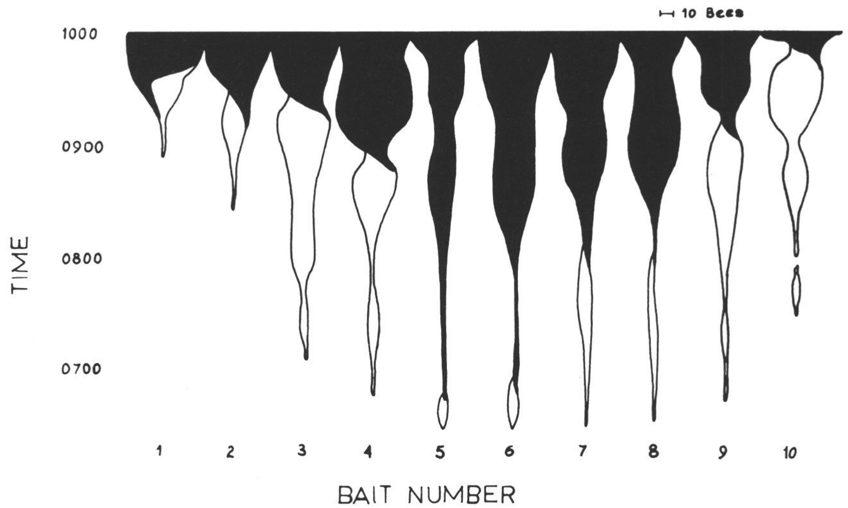

Fig. 10 – Visits by *Trigona fulviventris* (white) and a medium-sized black *Trigona extirpator* (black) to moist sugar baits 10 meters apart in the wet forest of the Osa Peninsula.

Fig. 10 – Visitas de *Trigona fulviventris* (blanca) y una extirpadora negra de tamaño mediano *(Trigona* sp.) (negra) a cebos de azúcar mojados, apartados 10 m en el bosque muy húmedo tropical de la Península de Osa, Costa Rica.

A similar temporal pattern was observed with *Trigona fulviventris* and a different extirpator in a wet forest habitat on the Osa Peninsula, August, 1970 (fig. 10). Of 84 sucrose baits, *T. fulviventris* was the first at 75 of them, and the extirpator was the first at 7 of them. Figure 10 shows one transect of sucrose baits placed 10 m apart. *T. fulviventris* recruited first, followed by the extirpator, who took them over one by one. In this experiment, on baits 4 and 9, *T. fulviventris* fought, but lost badly. Eight years later almost to the day I repeated the experiment at Corcovado, Osa. Again the pattern unfolded. *T. fulviventris* found the line of baits first, and was pushed toward the ends by the later arriving black extirpator. This time, however, I kept elongating the transect by adding new sucrose baits at the ends. On the new baits *T. fulviventris* found a temporary refuge (Johnson, unpubl.). An environment that would select for opportunism would be one with lots of small resources and rare, large, high quality resources of transient availability, transient either because they bloom briefly or because they are taken by a superior, aggressive group foraging competitor.

COMMUNITY STRUCTURE

Stingless bees are foraging generalists, collecting from a variety of plant species (Michener, 1954 ; Heithaus, 1979). This means that different species at a site can show extensive overlap in the plant species they visit (Johnson, 1974). Despite their broad preferences, New World stingless bees are food-limited, at least seasonally or intermittently (Johnson, 1974 ; Roubik, 1980, 1981) ; i.e., if more food were more easily accessible, colonies could reproduce more often. In some cases nest sites probably limit stingless bees, particularly in habitats devoid of the big trees some species require, but Hubbell and Johnson (1977) found no evidence of nest site limitation in a .367 km^2 tropical dry forest site.

If stingless bees species compete chiefly for taxonomically shared food resources, as their use of well-developed interference techniques at food sources suggests, it becomes of interest to know how the resources are partitioned. Since different species of stingless bees have foraging behaviors best suited for resources exhibiting particular dispersions in space and time, it is theoretically possible for competing species to stably partition resources according to dispersion. Johnson and Hubbell (1975), for example, found that an aggressive group foraging *Trigona* and a solitary foraging *Trigona* coexisted on one resource species for several weeks, utilizing clumps and isolated individuals of the plant respectively. The authors presented a graphical model demonstrating the feasibility of what they termed «density specialization». We are now ready to ask whether the complementary of foraging strategies is important enough to structure not only the interplay of particular colonies at resources, but to structure stingless communities themselves. As a null hypothesis one could imagine that community composition arises entirely from historical «accident», in a manner like that proposed by Hubbell (1979) for trees, or MacArthur and Wilson (1967) for island faunas. Bees emigrate at varying rates into a locality from adjacent source areas ; the probability of establishment of a species depends only on saturation of the community. The number of colonies of a species increase or decrease stochastically, and sometimes a species «random walks» to local extinction. Foraging behavior would not affect community structure, because the foraging flexibility of stingless bees (e.g., small, solitary bees can be avoiders, gleaners, or insinuators) would permit coexistence of any bee species with any other.

Alternatively, bee communities, given an equable temperature regime (Darchen, 1973) and a wide range of tree sizes for nesting, could be competitively rather than accidently structured. The probability of persistence of an emigrant into a community would depend on the resource structure and the foraging attributes of its rivals. Competitively important foraging traits could be the ones designated here, such a colony size, body size, aggressivity, and mode of communication, as well as others brought up by Roubik (1980), namely, ability to store food for periods of dearth, and size of foraging range as dictated by flight energetics.

Evidence for competitive structure occurs at least on the scale of a few hundred meters. Hubbell and Johnson (1977) found that the three *Trigona* species in a tropical dry forest that had large colony sizes and could recruit quickly to a precise location were the ones that had uniform spacing of nests, inter- and intraspecifically. Such a pattern could arise if the probability of establishment of a new colony of one of these three species was a function of its distance from existing colonies of these species. The question of whether foraging strategies structure stingless bee communities can be approached in several ways. One is to study the effect of an invading species on the composition it invades. If the relative proportions of the native foraging types are not systematically altered, one could not reject the null hypothesis. Roubik (pers. comm.) has undertaken such a study in Panama, measuring colony growth and reproduction, and foraging patterns of different kinds of stingless bees before and after the predicted arrival of the Africanized honeybee. Another possibility is an island biogeography study. One could record species composition in a tropical dry forest source area and in habitat islands of forest in a savanna «sea», and compare the communities with those predicted by the historical accident model. Finally, one could establish artificial communities on tropical islands uninhabited by stingless bees, beginning with species combinations predicted to be most and least compatible. Success of a species could be more finely monitored if observation hives were used, and results better interpreted if resources were controlled or characterized.

The study of stingless bees, however pursued, should be pursued quickly. Although much remains to be learned about traits of stingless bees and their adaptive significance, the neotropical forests that now support the largest assemblage of eusocial bees in the world are fast disappearing.

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COMPARATIVE FORAGING BY NEOTROPICAL ARMY ANTS

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SUMMARY

The army ants (Ecitoninae) include about 150 species, and most lowland Neotropical moist forests have about 20 sympatric species. Although the most noctural and subterranean species are less frequently seen by people, they are probably at least as abundant as those which are active on the surface of the ground during the day. The frequency of finding common species of Ecitoninae is given for 748 colonies at one locality in Panama and one in Ecuador. Most species of army ants feed primarily on ants. Workers of army ants range from 13 mm to 1.75 mm in length, and their prey ants range up to 1.5 times the length of the largest army-ant workers. No army-ant species preys on another species of army ant. The second most important group of prey are social wasps (Vespidae : Polybiini). A few species of army ants capture many groups of insects, other arthropods, and annelids. Among the species of potential prey with effective defenses against army ants are stingless bees, millipeds, and ticks. An average colony of *Eciton hamatum* has about 150,000 workers, a brood of 60,000 larvae, and may collect 90,000 insects per day. Based on the abundance of these ants and their high food consumption, they must have considerable effect on the prey species. The army ants do not kill colonies of social insects but only crop the colonies. Most of the adults from an attacked nest are not injured and continue the colony. Although our knowledge of the food of army ants is still very incomplete, we are convinced that there is enough prey specificity that several samples of prey from any species of Ecitoninae would be sufficient to identify a species of army ant.

RESUMEN

Comparación del abastecimiento de las hormigas guerreras neotropicales

Las hormigas guerreras (Ecitoninae) incluyen cerca de 150 especies, y la majoría de los bosques neotropicales y húmido de baja elevación tienen cerca de 20 especies simpátricas. Aunque las especies nocturnas y subterráneas son menos visibles, son probablemente tan abundantes como las que son activas durante el día en la superficie. El número de 748 colonias en una localidad de Panama y una de Ecuador nos da la probabilidad de encontrar especies comunes de Ecitoninae. Las mayoría de las especies de hormigas guerreras se alimentan principalmente de otras hormigas. Las obreras de hormigas guerreras miden de 13 mm a 1.75 mm de longitud, y alcanzan a capturar hormigas que tienen hasta 1.5 veces la longitud de las más grande de entre ellas. Ninguna especies de hormiga guerrera consume otra especie de hormiga guerrera. El segundo grupo más importante de presas son las avispas sociales (Vespidae : Polybiini). Unas pocas especies de hormigas guerreras capturan muchos grupos de insectos, otros artrópodos y anélidos. Entre las especies de presas potenciales con defensas efectivas son las abejas melipónidas, los milpiés y las garrapatas. Una colonia promedio de *Eciton hamatum* tiene cerca de 150,000 obreras, una cría de 60,000 larvas, y puede llegar a cazar hasta 90,000 insectos por día. Basado en la abundancia de estas hormigas y su gran consumo de alimento, se supone que dében de tener un efecto considerable sobre las especies que predan. Las hormigas guerreras no matan las colonias de insectos sociales : solamente las explotan. La mayoría de los adultos de un nido dañado no son eliminados y la colonia sobrevive. Aunque nuestro conocimiento del alimento de las hormigas guerreras es todavía muy incompleto, estamos convencidos que es bastante especifico, de tal manera que varias muestras de presas de alguna especie de Ecitoninae sería suficiente para identificarla.

INTRODUCTION

Ants have the most diverse food habits of all the groups of social insects, but individual ant species may be broad or highly specialized in their diet. Although army ants are frequently described as eating everything in their path, it is obvious that army ants cannot and do not eat everything. Many entomologists, however, still believe that all army ants are extreme generalists, eating all types of insects and other small animals. Furthermore, even biologists with long experience in the tropics are surprised to learn that a tropical forest may have about 20 sympatric species of army ants. This immediately raises the question of how so many «generalist» predators are able to co-exist. In this paper we will compare the raiding behavior and diet of sympatric army ants most of which are the same dominant species in all moist lowland tropical forests from southern Mexico to southern Brasil. Our research has been concentrated at two study sites each of which was visited several times during different years. One site is Barro Colorado Island in the center of Gatun Lake, Panama. The second site is Limoncocha, Ecuador (00° 24' S, 76° 36' W) on the western edge of the Amazon Basin at an elevation of 280 m. Both sites are lowland, moist, evergreen tropical forests. Barro Colorado has a distinct annual dry season, whereas, Limoncocha lacks a predictable and distinct dry season.

Table I – Genera and number of species of Ecitoninae and Dorylinae

Tabla I – Género y número de especies de Ecitoninae y Dorylinae

Ecitoninae	No. of species	Dorylinae	No. of species
Ecitonini		Dorylini	
Eciton	12	*Dorylus*	54
Labidus	8		
Nomamyrmex	3	Aenictini	
Neivamyrmex	117	*Aenictus*	50
Cheliomyrmecini			
Cheliomyrmex	5		
Total	145	Total	104

Army ants are distinct from other ants in that they have huge colonies, are highly migratory, and they capture invertebrates by group raids. Although other ant species share those characteristics, none has all of them and no other ants have such regular emigrations or predatory raids. All species of army ants have usually been included in one subfamily, the Dorylinae, but it is more correct to place the Neotropical and Nearctic species in the subfamily, Ecitoninae (Table I). The following discussion will be limited to the Ecitoninae.

ARMY ANTS AS GROUP RAIDERS

All species of Ecitoninae have large colonies with a minimal size of about 25,000 and a maximum of somewhat over one million. A new colony is established only when a colony has grown large enough to produce a brood of reproductives and to divide into two daughter colonies. All species are exclusively carnivorous, with the minor exception of *Labidus* spp. which occasionally feed on seeds or nuts high in oil. Group-raiding is considered to be an important adaptation allowing army ants to capture prey larger than themselves and also to raid social insect colonies which have considerable defensive capability (Wilson, 1958). Because of their large colony size and carnivorous habits, army ants must be migratory in order to find adequate prey near their nest. Unlike many ants which can store food such as seeds or liquids high in sugar content, army ants have no means of storing food. Consequently, large raids for food must occur almost daily for all tropical species. All worker army ants are blind but are sensitive to light. They locate their prey largely by random search, but raiding direction is heavily influenced by topographic features. A chemical trail is deposited wherever the ants run, and they are totally dependent upon that trail to find their temporary nest or bivouac. When the ants locate a good source of food, they employ a recruitment system that quickly attracts hundreds to thousands of workers to the food source (Chadab and Rettenmeyer, 1975).

Subterranean and epigaeic activity

Army ants can be classified according to the strata in which they are most active. Some species have been called epigaeic because they nest, raid, and emigrate on or above the surface of the ground. All other species have subterranean nests, but columns are often on the surface of the ground. Even the most subterranean species may occasionally be forced to have exposed columns if they encounter impenetrable soil. Highly subterranean species tend to have nocturnal columns or columns hidden under leaf litter or vegetation. When *Labidus* spp. have surface columns, the ants often cover the columns with a tunnel of loose soil. The most epigaeic raiders, especially *Eciton burchelli* and *E. hamatum*, raid to the top of the tallest canopy trees. Other species, such as *Labidus praedator*, usually stay on the ground but may go 2-3 meters up into the vegetation. The raiding strata obviously influence the kinds of prey encountered, and even when columns are restricted to the surface of the ground, subtle differences in prey may result because some army-ant species tend to go under leaf litter more than others.

The strata of activity of army ants has a large influence on their relative abundance as perceived by investigators. Studies of army ants have of necessity concentrated on the species which are most epigaeic, *Eciton* spp., and the extent of subterranean activity has been ignored or grossly underestimated. The best estimate available for the amount of subterranean activity is based on a comparison of the numbers of colonies of Ecitoninae found at our two study sites (Table II). These data and others for different localities in Central and South America indicate that any similar lowland moist tropical

Table II – Number of colonies of army ants found in two lowland moist tropical forests.

Tabla II – Número de colonias de hormigas guerreras encontradas en selvas tropicales de áreas bajas y húmedas.

	Panama		Ecuador	
	No.	%	No.	%
Eciton ssp. total	137	63.7	216	40.5
burchelli	23	10.7	27	5.1
hamatum	49	23.8	51	9.6
drepanophorum			2	0.4
lucanoides			35	6.6
dulcius	13	6.0	10	1.9
vagans	15	7.0	27	5.1
mexicanum	37	17.2	32	6.0
rapax			32	6.0
Labidus spp. total	43	20.0	224	42.0
praedator	34	15.8	108	20.3
coecus + sp. 1	9	4.2	116	21.8
Nomamyrmex total	15	7.0	33	6.2
Neivamyrmex total	20	9.3	60	11.3
Total	215	100	533	100

forest can be expected to have about 20 sympatric species of army ants. The species, *Eciton burchelli, E. hamatum,* and *E. lucanoides* typically emigrate, raid, and bivouac on or above the surface of the ground. Those most epigaeic species comprise 21-35 % of the army ant colonies found (Table II). Although all other species have subterranean nests, raid and emigration columns of all *Eciton* species are typically epigaeic. The *Eciton* species have the most conspicuous columns partly because the ants are the largest, ranging from 3-13 mm in body length, they carry the largest prey, and columns are sometimes 5-8 ants wide. Most workers in the other genera range from 6 mm, down to 1.75 mm in body length, and narrow columns 1-3 ants wide are typically partially or completely hidden by litter or vegetation.

Although we have found no exclusively subterranean workers in Central America or Ecuador, in the United States several species of *Neivamyrmex* are known whose workers are apparently exclusively subterranean in all activities. Nests or columns of some very common species have never been found. The ants are known to be abundant because clusters of ants can be found under stones, and males frequently fly to lights. Since there are also about 25 more species of male Ecitoninae described than there are workers for which no male is known, these unassociated males probably belong to highly subterranean species.

All species of *Labidus* probably do much raiding underground ; and even when they raid on the surface, their columns connecting to the bivouac are subterranean. Both raid an emigration columns sometimes were found extending only 10-100 cm on the surface. Thus, Table II is essentially a summary of epigaeic activity seen and not an accurate measure of the numbers of colonies present in those habitats. Nonetheless, the abundance of *Labidus* colonies ranged from 20-42 % and *Neivamyrmex* and *Nomamyrmex* together ranged from 16-18 % despite the fact that we also were more active on the surface of the ground during the day. Therefore, we conclude that colonies of *Labidus, Nomamyrmex*, and *Neivamyrmex* are at least twice as abundant as indicated in Table II, and comprise 60-76 % of all army-ant colonies.

Effect of activity cycle on raiding

The most extensively studied tropical army ants are *Eciton hamatum* and *E. burchelli* both of which have precise activity cycles first described by Schneirla (1933, 1973) (Fig. 1). Raiding is directly correlated with these cycles. During the statary phase lasting about three weeks, the colony remains in one bivouac, and the queen becomes physogastric and lays a huge brood of 25,000 to 100,000 eggs. Since the previous brood is in the pupal stage, enclosed in cocoons, there are no larvae requiring food. Consequently raids during the statary phase are short in distance and duration, and the food collected indicates the basal consumption rate to sustain the adult population under minimal activity levels.

The young callow workers emerge from their cocoons during 24-48 hours at the same time the eggs of the next brood are starting to hatch. The stimulation from those young adults is thought to be the primary trigger initiating the nomadic phase in which the colony emigrates nightly for a 2-week period. Throughout the nomadic phase the colony has greatly increasing requirements because the larvae, synchronized in age, consume more as they grow. In addition, the old adults must eat more to sustain their higher level of activity, and the brood of 25,000 to 100,000 young adults eat but do not participate in collecting prey during the first half of the nomadic phase. At the onset of the nomadic phase, raids typically start about 6:00 A.M. and end between 3:00 and 6:00 P.M. as the emigration begins. At the end of the nomadic phase, raids start at about the same time but continue until 6:00 to 10.00 P.M., with prey being carried to the new bivouac for several hours after the emigration has begun.

Considering the amount of prey brought into the nest, it is surprising to find so little food when bivouacs are sampled or examined. The insect prey

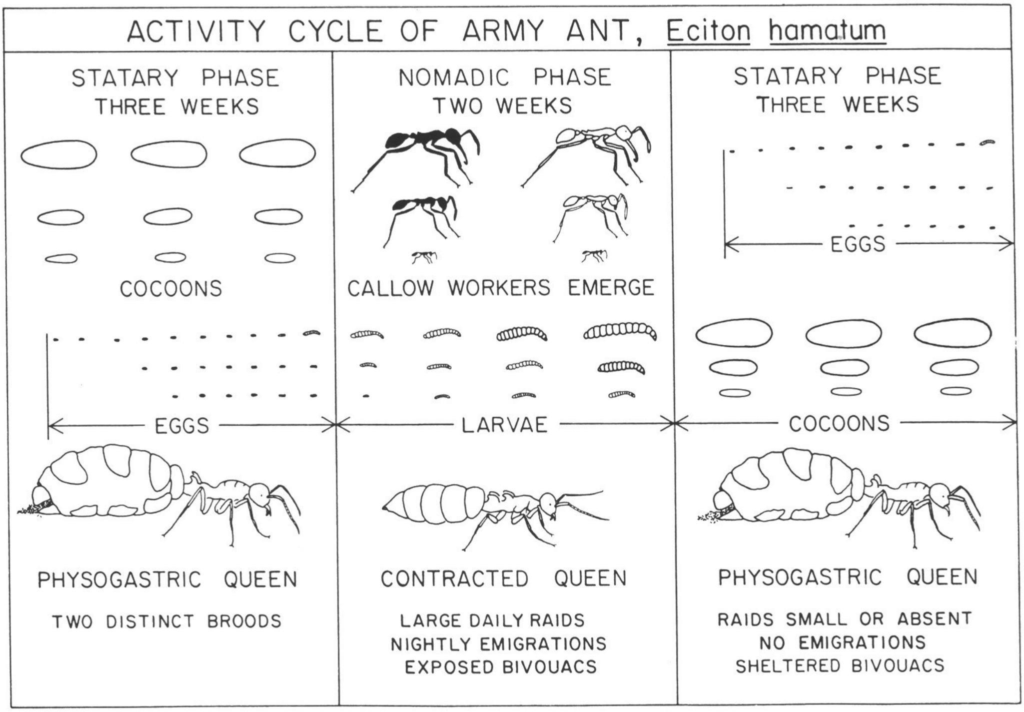

Fig. 1 – Activity cycle in *Eciton hamatum*

Fig. 1 – Ciclos de actividad en *Eciton hamatum*

is not stored, and most is consumed within a few hours so it is not transported to the next bivouac. During the nomadic phase *Eciton hamatum* typically has three base raid columns radiating from its bivouac (Fig. 2), and one of these becomes the emigration route. From counts of ant traffic on these columns it is possible to estimate the amount of prey collected during the day. When the emigration starts, prey seen coming out the emigration column from the old bivouac includes mostly prey that just came in on the other two raid columns. Prey numbers can also be estimated from the prey carriers on the emigration column near the new bivouac, but care must be taken to distinguish between prey ant larvae and the larval brood of the army ants carried in the same manner. Fortunately, army-ant larvae can usually be recognized by their elongate shape in contrast to the more plump shape and frequently larger size of the prey species. Estimates of daily prey intake by this method are further complicated because much of the prey is not brought directly back to the day's bivouac but deposited in the prey caches along the raid columns. Each temporary cache may contain over 1,000 pieces of booty guarded by workers and soldiers. It saves the ants considerable energy to deposit prey in caches, partly because that prey in caches near the new bivouac need only be carried a relatively short distance in the emigration and partly because the raiding ants can go back immediately for additional prey.

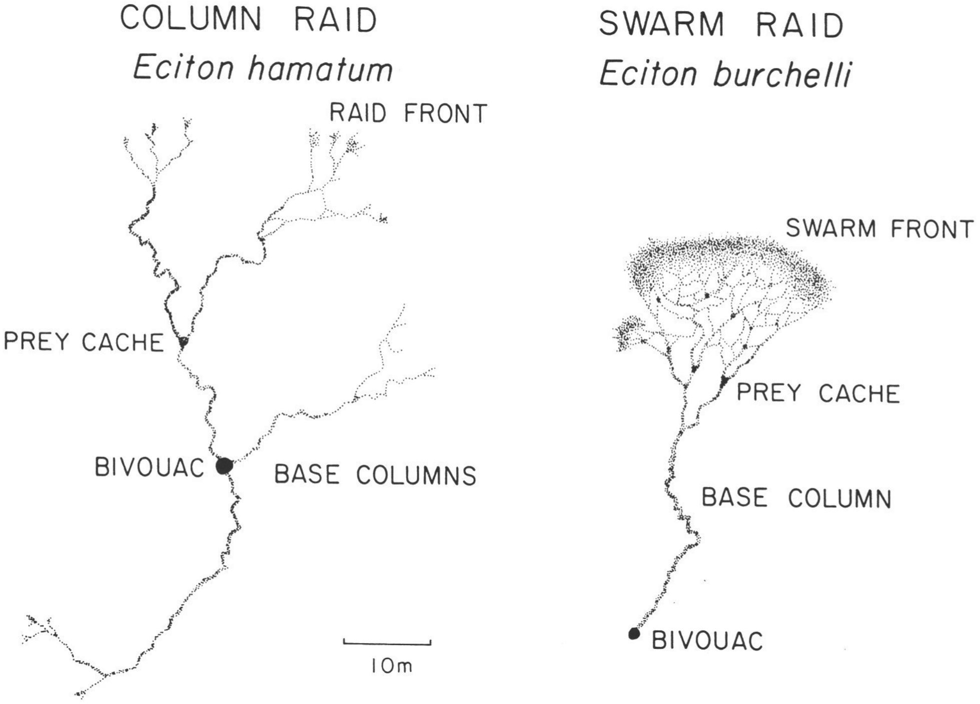

Fig. 2 — **Structure of the raids of two species of *Eciton*.**

Fig. 2 — **Estructuras de las correrías en dos especies de *Eciton*.**

During emigrations of *E. hamatum* the rate of ant traffic flow may be 25-50 ants per second. That is too fast for accurate counts, especially when prey carriers must be distinguished from those carrying brood, and unladden ants going in both directions must also be counted. The best technique we have used consists of filming the column with a 16 mm camera at 48-64 frames-per-second, for 5-sec intervals every 30 min (or sometimes more frequently when there is great fluctuation in traffic). Accurate counts can then be made when these films are projected at a reduced speed. In order to obtain the most complete coverage of the colony including estimates of prey brought to the new nest, it is essential to film within a few meters of the new bivouac as soon as it is possible to locate it. Although the technique sounds simple, there are so many practical problems that we have only obtained good records for eight emigrations and partial records for 14 others.

FOOD OF ARMY ANTS

Prey of Eciton hamatum

E. hamatum feeds almost exclusively on ant brood, but the species attacked in Panama vary from those attacked in Ecuador even when the same or similar species are present at both locations. Although attines are common in both localities, these ants were rarely raided in Ecuador but commonly raided in Panama. Formicinae, followed by Dolichoderinae, make up the largest biomass of prey in Ecuador. The formicines *Gigantiops destructor* and *Camponotus* spp. were represented in 54 % and 64 % respectively of 154 samples of prey of *E. hamatum* in Ecuador. In these same samples the dolichoderines *Hypoclinea* and *Dolichoderus* were found in 87 % and 45 % respectively and the myrmicine *Pheidole* in 48 % of the samples. Ponerines are less commonly raided than the previous three subfamilies, and the genera raided most commonly are *Pachycondyla* (= *Neoponera*) and *Anochoetus*. *E. hamatum* usually only captures a portion of an ant colony that is attacked. When the army ants attack, workers of the attacked species typically rush out of the nest carrying their brood. These ants may disperse over many meters, often going into the canopy of trees where they usually escape capture. After the army ants depart, the escapees return to their nest with the brood they carried out and continue colony activity. For at least one species, *Dolichoderus rugosus*, the odor of one crushed worker of *E. hamatum* is enough to cause a mass evacuation. *E. hamatum* seldom brings back adult ants to its bivouac. These not only resist or evade capture but are difficult for both the army-ant adults and larvae to eat, and many pieces of adults are discarded uneaten on refuse deposits. We have even seen a worker of *hamatum* carry an adult ant out of a nest in a stem and drop the ant before going back inside the nest, presumably to obtain some brood. Along with the ant brood, the army ants bring in Membracidae which are tended by *Pheidole*, but we do not know whether the army ants eat the Homoptera. Although a few other parasites or myrmecophiles show up is samples, all these nonsocial insects make up less than 0.01 % of the prey.

Next to ants, social wasps (Vespidae : Polybiini) are the second most important food source for *E. hamatum*. Most adults escape when the ants attack, but any remaining in or on the nest are captured. The odor of army ants is detected by some of the wasps and directly or indirectly triggers evacuation of the nest before numerous ants can overwhelm the colony (Chadab, 1980). Although social wasps make up only about 0.5 % of the pieces of prey brought in by *E. hamatum*, in biomass dry weight the wasps are 2-10 % of the total prey. As a result of the escape behavior of both ants and wasps, army ants do not eliminate colonies but interrupt their growth.

Prey of other Eciton species

E. lucanoides, which morphologically is the column-raider most closely related to *E. hamatum*, also has the most similar prey. Likewise, the two closely related species *E. dulcius* and *E. vagans* have great overlap in prey species. Both the latter species concentrate to a high degree on Ponerinae, especially *Odontomachus* spp., which appear to be avoided by *E. hamatum*. The smallest of the *Eciton* species, *E. mexicanum*, also seems to concentrate on Ponerinae, especially *Ectatomma* spp.

The workers of *Eciton rapax* are the largest of any Ecitonine (13 mm) and the only species of *Eciton* which does not have a distinct soldier caste. All soldiers of the other *Eciton* spp. have huge hook-like mandibles used for defense but not for capturing nor carrying prey. The largest workers of *E. rapax*, however, are not restricted to colony defense but actively participate in all aspects of raiding and emigrating. *E. rapax* preys primarily on large species of Ponerinae including *Pachycondyla crassinoda*, the largest ant we have seen regularly captured by any army ant. *P. crassionoda* is 18 mm long or 5 mm longer than the longest *E. rapax* workers, and it has a bigger sting and larger mandibles than the army ants. We do not know if it can ever successfully defend its colonies against *E. rapax*.

The last *Eciton* species we studied, *E. burchelli*, is completely different from the other species in its raiding behavior. It has swarm raids in one direction from the bivouac (Fig. 2). That type of raid covers the surface of the ground and much of the vegetation more thoroughly than a column raid. As a consequence the ants flush out a tremendous diversity of invertebrate and vertebrate animals. The advancing swarm is more efficient at capturing grasshoppers, crickets, spiders, and other active arthropods. Although *E. burchelli* captures arthropods as large or larger than the smallest workers and on rare occasions will even kill a small vertebrate such as a lizard, ants and social wasps still make up about 50 % of its diet. Since identification of the prey of *E. burchelli* is tantamount to identifying all the species of large arthropods in a tropical forest, analysis of *E. burchelli* has not progressed far. It is perhaps more fruitful to mention a few of the species avoided by *E. burchelli.*

Arthropods not captured by Eciton spp.

All ticks and millipeds are apparently adequately protected by their defensive secretions. However, the defensive chemicals of Hemiptera usually are not effective, and Reduviidae, Pentatomidae, and others are captured by *E. burchelli.* Many caterpillars are protected if they are covered with dense or long hairs. Phalangida have such thin legs that the ants have difficulty climbing them. If an ant gets on a leg, the daddylonglegs shakes it off, sometimes standing on fewer and fewer legs until it gets down to three when it will run off. Spiders can escape by dropping on a strand of silk which the army ants will not descend. Some beetles such as Scarabaeidae are so armored that they cannot be dissected by *E. burchelli* even in several hours of intensive effort. Some beetles are greatly incapacitated by the army ants since the legs may be injured or tarsi removed so the beetle has difficulty walking. We have never seen a butterfly captured by *E. burchelli*, but some fast-flying insects that would seem to be immune have been killed. For example, adult flies and even dragonflies are sometimes caught by the ants. Termites which are so well represented in tropical forests would seem to be an excellent source of food for army ants, but we know of no common species that raids them. All the *Eciton* species we have seen encounter *Nasutitermes* and a few other termites have been repelled by the termites' defensive secretions or odors. The other main group of tropical social insects, the Meliponini or stingless bees are also not raided. We have seen *Eciton* spp. approach colonies of *Trigona* and *Melipona* and occasionally run into the entrance tubes of the bees. The bees attack the ants and daub them with stickly propolis. The army ants in every case were able to capture only one to a few adult bees.

Prey of Labidus spp.

Labidus praedator has swarm raids which resemble those of *E. burchelli* except that the ants are smaller (workers 2-7 mm in comparison to 3-10 mm) and capture smaller prey. *L. praedator* can also capture prey many times its size such as cockroaches, but the majority of prey are much smaller such as Homoptera. *L. praedator* is highly subterranean and raids extensively under litter where it captures many isopods and amphipods. Other species of *Labidus* are more subterranean than *L. praedator*, and we know less about their prey. They do capture beetle larvae that would not be found by *E. burchelli* because the larvae live in litter or soil.

Prey of Nomamyrmex **spp.**

Nomamyrmex esenbecki has been considered most closely related to *Labidus* on morphological grounds, and those two genera have the most similar guests living within their colonies. From the standpoint of its raiding, *N. esenbecki*, is similar to an *Eciton* species because it has epigaeic column raids and attacks similar prey. Although it raids many kinds of ants and occasionally social wasps, it seems to concentrate more than any other army ant on raiding *Odontomachus*. A spectacular subterranean raid by *Nomamyrmex esenbecki* on *Atta mexicana* was incidentally observed and filmed in February 1970 in Ajijic, a locality on the northern border of Chapala Lake, Jalisco, Mexico. The leaf-cutter nest had been excavated to a maximum depth of 3.5 meters to permit filming of the nest interior and during the course of the filming the *Nomamyrmex* attacked at a depth of 1-2 meters. The army ants carried off many thousands of larvae, pupae, and callow workers and killed many adult ants including the queen. No army ants were active on the surface of the ground, and the entire raid would not have been detected if the excavation had not been dug in order to film the leaf-cutters. (The film «Les Fourmis Tropicales» was shown as part of this symposium, and Dr Pierre Jaisson, one of the observers, kindly provided additional information).

We have not been able to find workers of the other two species of *Nomamyrmex*, but it is noteworthy that there are two records of *N. hartigi* feeding on termites in Panama and Brasil (Rettenmeyer, 1963). The ants were found raiding up covered termite tunnels on tree trunks and bringing down termites. That is the only Neotropical army ant suspected of specializing on raiding termites, but some North American *Neivamyrmex* regularly eat them as well (Pullen, 1963).

Prey of Neivamyrmex **spp.**

The genus *Neivamyrmex* includes 117 species, but each *Neivamyrmex* species has a more limited geographical range than the common species in the three genera of army ants discussed above. We have few prey records, but these suggest that *Neivamyrmex* species concentrate on small species of ants.

N. pilosus, for example, repeatedly has been found raiding *Crematogaster*, a genus of myrmicine ants which seems to be avoided by *Eciton* species. Two species, *N. pseudops* in Panama and *N. diana* in Ecuador, raid *Pseudomyrmex*. All army ants raid species of ants which range from the size of the smallest army ant workers of the species up to 1.5 times the length of the largest workers. Thus, there is a general correspondence between the size of the prey and the size of the predator. One of the primary advantages of the extreme polymorphism exhibited by many army ant species is that the different size of ants are adapted to handle different sizes of prey. Although army ants capture some ants considerably smaller than themselves, such as *E. hamatum* preying upon *Strumigenys*, it is rare that they do so. We assume that most *Neivamyrmex* species specialize on small ants, a conclusion substantiated by 15 tropical species and three species of *Neivamyrmex* we have observed in Kansas.

PREY SIZE AND BIOMASS AND INTERACTIONS BETWEEN PREDATOR AND PREY

It appears that for every species of ant known in a tropical forest there exists an army-ant species of appropriate size to raid it with one exception. The largest ponerine in Panama and Ecuador, *Paraponera clavata*, does not seem to have an effective army-ant predator (unfortunately !). That ponerine is common at both localities, and we have seen *E. burchelli* workers fight with *Paraponera* workers for hours, but the army ants were not successful in raiding the nests. Only one major subfamily of ants is never raided by army ants and that is the Ecitoninae. Regardless of the size relationships, no army ant of any species has been seen to injure or capture another army ant although whenever two species of army ants come in contact considerable innocuous nipping back and forth may occur. The amount of prey collected by a colony of army ants is directly related to both the size of the colony and the stage of larval brood present in the colony. All species have considerable variation in colony size, but atypically small colonies seem to be unable to maintain the raiding-emigrating behavior and probably cannot exist for more than a few months. Colonies of *E. hamatum* range from 50,000 to 250,000 adults and have an average size of about 150,000 with a brood of 60,000 larvae. Brood production is so high that adult mortality must also be high. Most of the mortality we believe is due to three factors : (1) mortality or severe injury when fighting with ants or wasps, (2) separation from chemical trails, or (3) exposure to high temperatures or severe rain during raiding or emigrating.

Estimates of prey numbers and biomass (dry weight) are given in Table III. These data show that the average strong raid brings in 15,000 to

40,000 prey per day. Maximum raids for *hamatum* may yield about 90,000 insects, including many minute ant eggs and larvae and few adults.

Table III – Estimates of prey carriers, numbers of prey, and prey biomass for *E. hamatum*

Tabla III – Estimación de hormigas transportadoras de presas, del número de presas, y de la biomasa de presas en *E. hamatum*.

Colony	Raid	Daily number	Total prey		Wasp prey	
phase	strength	prey carriers	number	biomass (mg)	number	biomass (mg)
statary	weak	2,000-5,000	3,000-7,600	1,070-2,680	18-46	130-330
statary	strong	10,000-35,000	15,200-53,200	5,400-19,000	91-319	650-2,280
nomadic	weak	5,000-10,000	7,600-15,200	2,700-5,400	46-91	330-650
nomadic	strong	25,000-60,000	38,000-91,000	13,400-32,200	228-547	1,630-3,920

The army ants must have a considerable effect on the prey species and may prolong the length of time for an ant or wasp colony to reach an adequate size to produce reproductives. Since the army ants do not kill ant or wasp colonies they are ecologically analogous to grazing animals. The army ants crop their social insect prey, leaving the adults to continue the colony and produce more brood for the next army-ant colony to collect. Although our knowledge of the food of army ants is still very incomplete, we are convinced that prey specifity is such that several samples of prey from any species of Ecitoninae would be sufficient to identify a species of army ant.

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A BEHAVIOURAL STUDY OF PREDATION BY SERRASTRUMA SERRULA SANTSCHI (FORMICIDAE, MYRMICINAE)

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SUMMARY

A behavioural analysis of Collembola capturing can be based on a succession of phases : detection, localization, approach, antennating, attack, stinging, transport. The richest sequence is most frequent when prey and predator meet one another by chance. Detection, approach and antennating are absent in fortuitous meetings and when the prey is inert there is prolonged antennating followed directly by transport of the prey. The behaviour of the ant is adjusted to the situation. After an unsuccessful attack, the worker is excited and mandibles remain open as during approach. If it then meets a living Collembola it attack and stings directly. If it meet an inert prey there is no antennating but stinging is very frequent (92 %). The behaviour of an excited ant is badly adjusted to this last situation : an excited worker generally carries out the end of the sequence even if it is not necessary.

RESUMEN

Estudio del comportamiento de predación de Serrastruma serrula **Sautschi (Formicidae, Myrmicinae)**

El estudio de las secuencias de comportamiento durante la captura de *Folsomia candida* por las obreras proveedoras de *Serrastruma serrula* nos permite distinguir la sucesión de las fases siguientes : detección ; localización ; marcha de approximación ; palpación antenal ; ataque ; picadura ; transporte. Cuando presa y depredador se encuentran por azar, la secuencia mas rica es la más frecuente. Cuando la proveedora encuentra fortuitamente un Colembolo, la secuencia conductal es siempre rápida, pues no existen las fases de detección, approximación y palpación. En presencia de una presa inerte, la palpación antenal es siempre de larga duración, la picadura no se ha observado más que excepcionalmente. Son adaptaciones a la situación. Cuando una proveedora está excitada por una fallida, conserva sus antenas dirigidas hacia adelante y sus mandíbulas abiertas. Si encuentra en ese momento una presa, la ataca directamente. Este comportamiento permitirá, eventualmente, encontrar la presa que ha huido y capturarla. Si se le da un Colembolo anestesiado con CO_2 a una proveedora excitada por una captura fallida, falta la palpación ; la picadura está presente en general. El comportamiento de la obrera se encuentra, pués, mal ajustado a la situación. Esto muestra que el fracaso excita a la obrera que tendrá, entonces, tendencia a desarrollar hasta el final la secuencia, incluso si no es necesario.

INTRODUCTION

Brown and Wilson, in 1959, during their study on the evolution of Dacetini, showed that Collembola make up the essential part of the diet for the species which belong to the subtribe *Strumigeniti* and that there exist a fundamental difference between the predatory behavior of species with long mandibles and those with short mandibles. *Strumigenys*, with long mandibles, after a short approach period, strikes the prey, after which there may or may not be a stinging phase. *Trichoscapa*, with short mandibles, approaches slowly and strikes an appendage of the prey. Stinging is obligatory. Our study is of the genus *Serrastruma* whose mandibles are intermediate between the two cases just cited. The genus *Serrastruma* has been derived from the *Smithistruma* which has short mandibles (Brown, 1952). The sequential analysis exposed in this work was systematically conducted with the prey being the Collembola *Folsomia candida*.

SEQUENTIAL ANALYSIS

Analysis of the behaviour phases during the capture of the Collembola *Folsomia candida* shows the following sequence : detection, localization, approach (with opening of mandibles), antennation, attack, lifting, stinging (fig. 1), transport. This is the whole sequence, but depending on the conditions one phase or another may or may not be present.

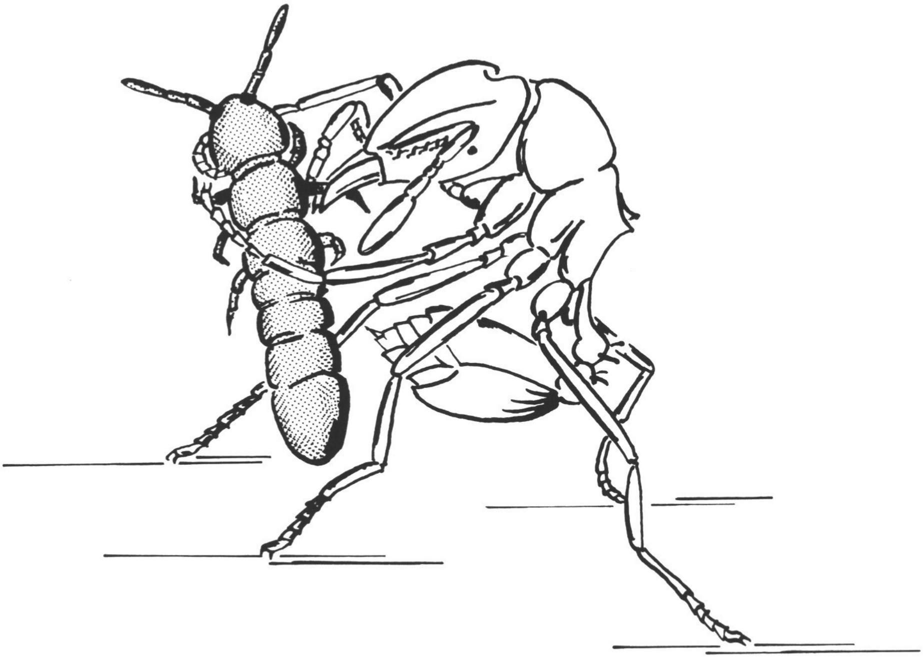

Fig. 1 – Stinging. The worker is standing on its mesal and hind legs between which the gaster is reflexed. It is preparing to sting the Collembola which is lifted up by a mesal leg. The forelegs of the ant seize the prey which is struggling.

Fig. 1 – Picadura. La obrera levanta al Colembolo por una pata, y manteniendo con sus patas anteriores la presa la cual forcejas, está a punto de picarla.

A study of the capture of *Folsomia* by the foraging workers *Serrastruma serrula* is shown in figure 2, where we can see that the prey can escape at different levels. The results are presented in Table I. We establish that the richest sequence is also the most frequent (50 %). It is followed by those alternatives where the closing of the mandibles and/or the raising of the prey are/is absent.

Rapid attack : in certain cases (16 %) antennating is absent. The whole sequence will be shorter, because this phase may be long (30 sec.).

Unexpecter encounter : sometimes the prey and the predator are going in different directions and run into each other unknowingly. Thus there is neither detection nor approach. Because of this it seems that the worker becomes excited, since all the actions which follow are hurrierd. There is no antennating. The striking action is always present.

Table I – Sequential analysis of the predatory behavior of one hundred foraging workers capturing living *Folsomia*.

Tabla I – Análisis secuencial del comportamiento de predación de 10 obreras proveedoras capturando *Folsomia candida* vivos.

% of presence	Phases	Richest sequence	Variations as a function of the richest sequence			Quickly attacks				Unexpected encounter		Slow or inert prey			
88 %	Detection	+	+	+	+	+	+	+	+	—	—	+	+	+	+
100 %	Localization	+	+	+	+	+	+	+	+	+	+	+	+	+	+
88 %	Approach	+	+	+	+	+	+	+	+	—	—	+	+	+	+
100 %	Openning of the mandibles	+	+	+	+	+	+	+	+	+	+	+	+	+	+
71 %	Antennating	+	+	+	+	—	—	—	—	—	—	—	+	+	+
	Attack														
78%	Stricking	+	—	+	—	+	—	+	—	+	+	—	—	—	+
79 %	Lifting of the prey	+	+	—	—	+	+	—	—	+	—	—	—	+	—
91 %	Stinging	+	+	+	+	+	+	+	+	+	+	—	—	—	—
	Percentage	50	7	2	4	10	2	3	1	9	3	1	6	1	1

Slow or inert prey : the last three phases are absent. After examining the condition of the prey during a long antennating period, the worker grasps it and takes it to the nest.

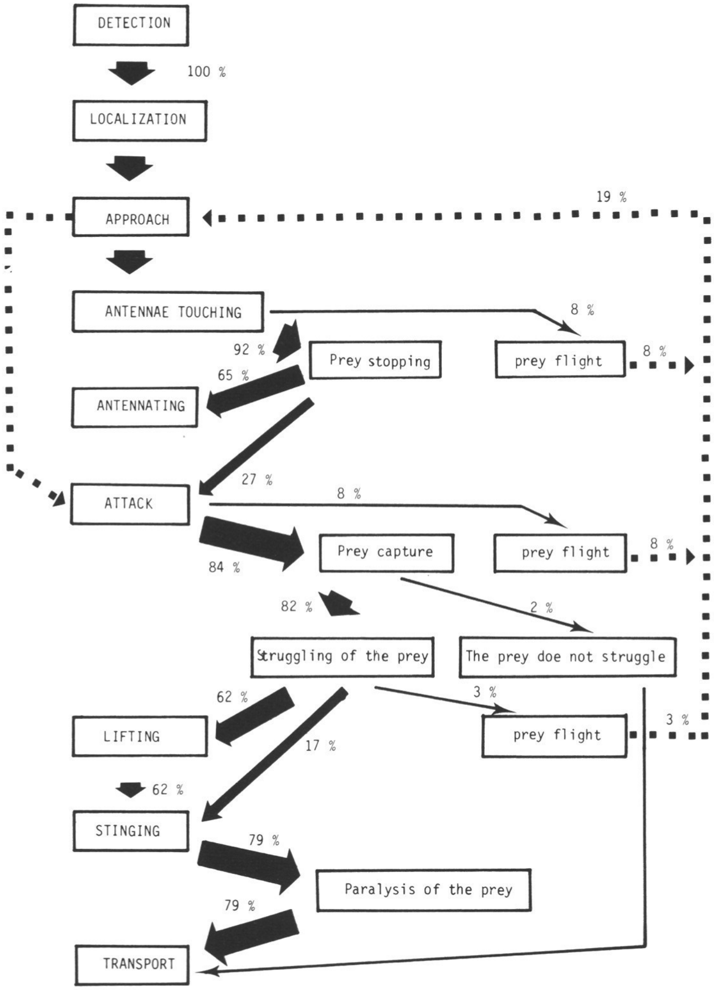

Fig. 2 – Schematic figure of the sequential analysis of predation behaviour of *Serrastruma serrula* ; the prey is the Collembola Isotomidae : *Folsomia candida.* Each arrow shows the passage between the differents acts. Its thickness is approximatly proportional to the percentage of observed cases.

Fig. 2 – Representación esquemática del análisis secuencial del comportamiento de predación de *Serrastruma serrula* capturando el Colembolo Isotomidae *Folsomia candida.* Cada flecha indica el paso de un acto dado al otro. Su espesor representa aproximadamente el porcentaje de casos observados.

SEQUENTIAL ANALYSIS AFTER EXPERIMENTAL INTERVENTION

We carried out a series of sequential analyses after changing certain variables. The results are presented in Table II. The foraging worker encounters a Collembola anaesthesized by CO_2. The antennating is exceptionnaly long and stinging is absent. The foraging worker, excited by the escape of its prey, meets another one which is alive and active : the worker moves swiftly, antennae pointed forward, mandibles open. This posture may last 45 seconds. When this worker meets the prey it is in such a state that it attacks and stings immediately. There is no antennating. The actions of the worker are hurried.

Table II – Sequential analysis of the predatory behaviour of foraging workers, in three situations

Tabla II – Análisis secuencial del comportamiento de predación de las obreras proveedoras dentro de tres situaciones particulares.

Phases	Inert prey given to foraging workers			Foraging workers excited by the escape of prey				Workers excited by the escape of prey encounter inert prey				
Detection	+	+	+	—	—	—	—	+	+	+	+	+
Localization	+	+	+	—	—	—	—	+	+	+	+	+
Approach	+	+	+	+	+	+	+	+	+	+	+	+
Opening of the mandibles	+	+	+	+	+	+	+	+	+	+	+	+
Antennation	very long			—	—	—	—	—	—	—	—	—
Attack Striking	—	—	—	+	+	—	—	+	+	—	—	—
Lifting of the prey	—	+	+	+	—	+	—	+	—	+	—	—
Stinging	—	—	+	+	+	+	+	+	+	+	+	—
Number of observed cases	37/40	2/40	1/40	18/32	12/32	1/32	1/32	10/24	5/24	4/24	3/24	2/24
Percentage	92,5	5	2,5	56,25	37,5	3,125	3,125	41	21	17	13	8

The foraging worker, excited by the escape of its prey, meets an inert one (anaesthesized by CO_2). For this experiment we excited the ant by presenting an anaesthesized Collembola on the tip of a fine paintbrush. The prey was removed before the ant could capture it and placed on the ground near the worker. As in the preceding cases, the worker, excited by the loss of this prey, moves swiftly, antennae pointed foward, mandibles open. When it finds the prey that we placed near it, the ant attacks immediately. Antennating is never seen. Although in 8 % of the cases the prey is transported directly to the nest, we did not observe complete adjustement of the behavior of the ant to this situation. This result illustrates the excited state of the worker after a failure.

CONCLUSION

Foraging workers of *Serrastruma serrula* can adapt there predatory behaviour in certain situations : unexpected encounter with the prey, which provokes a swift reaction ; detection of a dead or inert prey, which is followed by a long antennating period and then direct transport towards the nest (the phases which are not indispensable are absent). After a failure escape or loss of prey, attack is rapid and the stinging is carried out very early. The workers are adapted to the capture of Collembolans whose antipredatory tactics consists of immobility at contact with the predator. If the prey escapes, the ant has a second tactic which allows it to find and eventually capture prey. This second solution requires much more energy than the first.

It results in despecialization which will permit worker to capture other prey which systematically run away when the worker approaches. The worker in this excited state has a lot of difficulty in adjusting its behaviour when it encounters inert prey. In this case, the succession of actions leading to the typical capture (striking, raising, stinging) tends to be present, even though not necessary.

This compensating behaviour is important because it permits the *Serrastruma* to colonise areas where the population of collembolans decreases during certain seasons because its too dry. In this case the foraging workers capture other insects whose populations increase under dry conditions. This is observed under forest of Eucalyptus at the beginning of the dry season, where certain Psocids are abundant. Psocids do not freeze in front of *Serrastruma.*

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FORAGING AND MORPHOLOGY IN ANTS : THE ROLE OF VERTEBRATE PREDATORS AS AGENTS OF NATURAL SELECTION

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SUMMARY

Most recent studies concerning the ecology of foraging in ants have emphasized only the relationship between ants and their food resources. Though mainly speculative, this contribution suggests that ants' predators, notably lizards and anurans, may have had great importance in the morphological evolution and the ecology of foraging in ants. A simple theoretical model of the ecology of foraging is used to suggest some possible evolutive results as a consequence of predation. Data obtained on foraging ants on Barro Colorado Island, Panama, support some of these suggestions. Finally, a checklist of the possible evolutive results of predation on foraging ants is presented.

RESUMEN

Forrajeo y morfologia de las hormigas : papel de los Vertebrados depredadores como factores de seleción natural.

La mayoría de los estudios recientes sobre la ecologia del forrajeo en las hormigas han enfatizado solamente la relación entre las hormigas y sus recursos alimenticios. Este artículo, aunque en gran parte teórico, sugiere que los predadores de las hormigas, especialmente largartijas y anuros, pueden haber tenido gran importancia en la evolución de la morfología y la ecología del forrajeo de las hormigas. Se usa un modelo teórico simple de

la ecología del forrajeo en las hormigas para sugerir algunos posibles resultados evolutivos como consequencia de la predación. Datos tomados sobre hormigas abasteciendo en la Isla de Barro Colorado, Panamá, sustentan algunas de estas sugerencias. Sigue una lista de los posibles resultados evolutivos de la predación sobre el forrajeo en las hormigas :

1 – Las especies en las que las hormigas forrajean individualmente y que no tienen buenos métodos de reclutamiento no demuestran polimorfismo entre las obreras. Estas especies pueden resistir a la predación por medio de su tamaño grande, su agresividad, y sus armamentos ; o pueden escaparse por medio de su camuflage, su vida nocturna, o su tamaño pequeño.

2 – Las pequeñas legionarias forrajean escondidas o de noche ; las legionarias más grandes son agresivas y bien armadas. El forrajeo en columnas en estas especies puede estar más relacionado al abastecimiento que a la defensa contra los predadores. El polimorfismo de las obreras en las hormigas guerreras parece estar relacionado a la recolección de recursos.

3 – Los sistemas de defensa basados sobre las alomonas se encuentran generalmente en las hormigas monomorficas, de tamaño pequeño o medio, que frecuentemente tienen el tegumento suave y que forrajean en grupos. Las hormigas que usan alomonas como defensa frecuentemente son manifiestamente pastoras de afidos o recolectoras de nectar.

4 – Las hormigas que generalmente tienen pocas defensas contra los predadores, pero tienen un buen sistema de recolección, pueden emplear una estrategia de reclutamiento de obreras polimórficas.

5 – Las especies en las cuales las obreras mayores pueden desempeñar una función defensiva, pueden tener una estrategia de desplegar obreras polimorficas. El forrajeo en columnas en estas especies puede haber sido seleccionado como un componente importante de esta estrategia.

6 – El forrajeo en columnas también puede encontrarse en especies que solamente en grupos pueden resistir o rechazar a los predadores.

7 – El mimetismo, tanto Batesiano como Mulleriano, parece poder existir entre las hormigas. Con respecto a esto, el hecho que muchas otras familias de insectos y de arañas mimetizan a las hormigas, merece estudio, particularmente con relacion a sistemas de defensa contra predadores de las hormigas que sirven como modelo.

> *«I could never satisfy myself as to the function of these worker-majors. They are not the soldiers or defenders of the working portion of the community, like the armed class in the Termites, or white ants ; for they never fight. The species has no sting, and does not display active resistance when interfered with. I once imagined they exercised a sort of super-intendence over the others ; but this function is entirely unnecessary in a community where all work with a precision and regularity resembling the subordinate parts of a piece of machinery. I came to the conclusion, at last, that they have no very precisely defined function. They cannot,*

> *however, be entirely useless to the community, for the sustenance of an idle class of such bulky individuals would be too heavy a charge for the species to sustain. I think they serve, in some sort, as passive instruments of protection to the real worker. Their enormously large, hard, and indestructible heads may be of use in protecting them against the attacks of insect-ivorous animals. They would be, on this view, a kind of «pieces de resistance», serving as a foil against on-slaughts made on the main body of workers».*
>
> **Henry Walter Bates**
> *The Naturalist On the River Amazons*

Differences in foraging ecology among ant species are widely recognized (see Wheeler, 1910 ; Sudd, 1967 ; Wilson, 1971, and Carroll and Janzen, 1973, for reviews). Most studies of ant foraging ecology have emphasized either the integrative mechanisms of the behavior in a species (Wheeler, 1910 ; Sudd, 1967) or the exploitation of resources by a species or by several competing species (Carroll and Janzen, 1973). The recent general theoretical interest in optimal foraging theory (Pyke et al., 1977) reinforces these perspectives. An overview of these studies would suggest that the investigators' views on ant foraging ecology incorporate the relation between consumers (the ants) and resources as the primary determinants of foraging strategy in the ants themselves (Figure 1). Morphology and behavior in ants are therefore generally interpreted as components of a resource aquisition strategy.

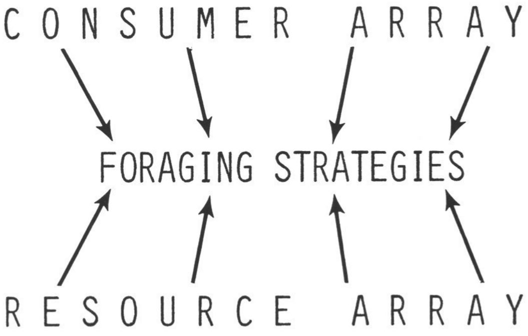

Fig. 1 – Most contemporary studies of ant foraging ecology imply that foraging strategies are the evolutionary result of only two main factors : patterns of resource aquisition and competition among ant species for access to resources.

Fig. 1 – Muchos estudios contemporáneos sobre la ecología del forajeo implican que las estrategias de las hormigas sean el resultado evolutivo de solamente dos factores principales : los patrones de fuentes de abastecimiento y la competencia entre las especies de hormigas para el aceso a los alimentos.

In my own field work with ants in the early 1970's (Hunt, 1977 ; Cody et al., 1977 ; Mares et al., 1977) I noted repeated instances in which it seemed that features of ant foraging strategy, including both behavioral and morphological components, could be interpreted in relation to potential predation by vertebrates that prey upon foraging worker ants. The most notable vertebrates in this regard are lizards and anurans. I did not form the opinion that vertebrate predation is the sole selective force acting on ant foraging strategy ; rather it seemed that an assessment of the potential role played by vertebrate predation could amplify and perhaps clarify an analysis based only on resource considerations. Two examples will clarify my position.

Two species of the formicine genus *Myrmecocystus* (honey pot ants) are abundant at a site I studied in southern California. One, *M. flaviceps*, is exclusively diurnal ; the other, *M. testaceous*, is exclusively nocturnal (Hunt, 1973). The complete separation of foraging times is in marked contrast to the broad overlap in habitats foraged and a probable broad overlap in resources taken. These sympatric congeners thus seem to be a good example of competitors for common resources that have undergone competitive displacement and now occupy disjunct ecological niches (Pianka, 1978). Particular behaviors of each species suggest a further interpretation, however. *M. flaviceps* is active at higher ground surface temperatures (up to 50° C) than any other ant species at the site. By rapidly darting from twig, to pebble, to grass stem, and so on, foragers can cover sites where workers of *Camponotus anthrax*, shaken from their arboreal foraging sites in shrubs, rapidly die from the heat. *M. testaceous*, the nocturnal species, offers a marked contrast. Large numbers of foragers congregate near nest entrances, standing or moving slowly about in a manner never seen in *M. flaviceps*. My interpretation of these behavior differences is that each species has adopted a strategy whereby it can avoid possible predation by the many lizards at the site. *M. testaceous* forages only at a time when the lizards do not ; *M. flaviceps* forages diurnally but over ground surfaces too hot to be traversed by lizards. It seems plausible to me to describe the observed foraging differences as alternative selected responses whereby each species avoids exposure to predation.

A second example involves the well studied New World harvester ants of the genus *Pogonomyrmex*. Hölldobler (1974) detailed the foraging habits of three species in southern Arizona. Two of these, *P. barbatus* and *P. rugosus*, utilize conspicuous trunk trails for foraging, and Hölldobler documented a closer intraspecific spacing of nests for these species than for *P. maricopa*, in which individuals forage without the use of trunk trails. Hölldobler's suggestion that foraging via trunk trails facilitates a finer partitioning of the area foraged than is possible with a more uniform dispersion of individual foragers is most likely correct. Upon inquiry, however, I learned that *P. barbatus* and *P. rugosus* can sting with a potency that is painful but not unbearable, whereas a *P. maricopa* sting borders on excruciating pain (R.R. Snelling, personal communication). I would suggest, then, that studies might reveal that individual *P. maricopa* can successfully repel predators while *P. barbatus* and *P. rugosus* can successfully do so only en masse. The foraging strategies and resource partitioning documented by Hölldobler thus may well reflect alternative strategies of predator resistance.

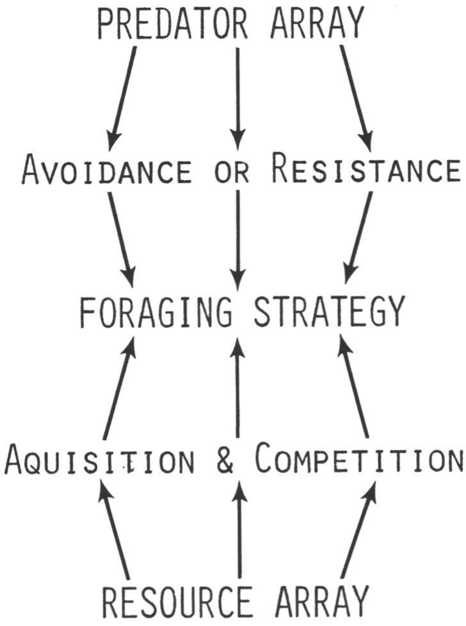

Fig. 2 – It is suggested that ant foraging strategies reflect composite adaptations to several selective pressures. Resource aquisition and competition for resources are, to be sure, important. However, some components of ant foraging strategies, including both morphological and behavioral features, may have been selected for as either avoidance or resistance responses to vertebrate predation.

Fig. 2 – Se ha sugerido que las estrategias de forajeo de las hormigas reflejan adaptaciones a varias presiones selectivas. La recolección de recursos y la competencia para ella son importantes. Sin embargo, algunos componentes de las estrategias del forajeo, incluyendo carácteres morfológicos y comportamentales, pueden haber sido seleccionado para evitar o resistir a la predación de los Vertébrados.

No predation data have been collected on either the *Pogomomyrmex* species studied by Hölldobler or on the *Myrmecocystus* species studied by me, but I feel that do so could both expand the traditional resource based interpretations of the observed foraging strategies and offer insight on the selective mechanism that may have fostered them. I suggest that a complete analysis of ant foraging ecology can be prepared only by simultaneous consideration of both response to predation and access to resources (Figure 2). In the remainder of this paper, then, I propose to speculate on some of the features of ant morphology and behavior that I believe can be interpreted in relation to predator selective pressure. As a first analysis I have prepared a very general classification of ant foraging ecologies that is based only on features of the foraging system itself (Figure 3). Relevant criteria are :

1 – whether workers of a species forage solitarily or in groups ;
2 – for those species that forage solitarily, whether recruitment to resources is lacking, poor, or good ;
3 – for group foraging species, whether the sought for resources are stationary (plants and detritus) or mobile (living arthropods) ; and
4 – for all species, whether the workers themselves are (1) monomorphic, (2) show monophasic allometry, or (3) exhibit complex polymorphism (see Wilson, 1971, for definitions and discussion).

Genera that exemplify various categories have been included in the Figure, and descriptive terms that correspond to each category are given.

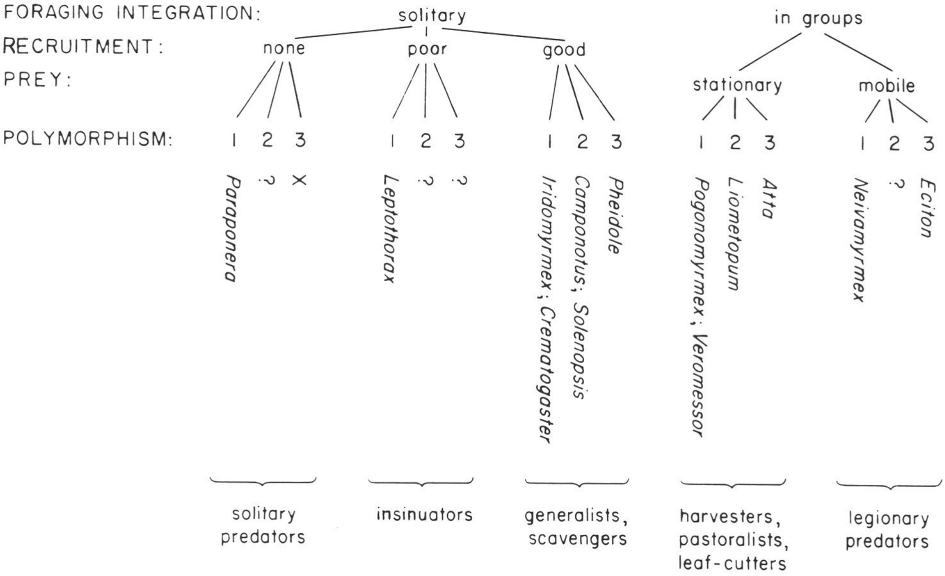

Fig. 3 – A scheme for identifying ecological categories of foraging in ants. The first distinction is whether ants forage solitarily or in groups. For ants that forage solitarily, distinction is made in degree of recruitment : no recruitment, poor recruitment, or good recruitment. For group foraging ants a distinction is made as to whether the sought for resources are stationary or mobile. Polymorphism in all ants is distinguished as 1) monomorphic ; 2) monophasic allometry ; 3) complex polymorphism.

Fig. 3 – Una esquema para la identificación de las categorias ecológicas del forajeo en las hormigas. Se considera primero si las hormigas forajean solas o en grupo. Para las primeras, se distingue el grado de reclutamiento : no reclutamiento, poco reclutamiento o buen reclutamiento. Para las hormigas que forajean en grupo, se distingue si la busqueda de recursos es estática o móbil. Se ha dividido el polimorfismo en todas las hormigas entre : 1) monomórfico ; 2) alometría monofásica ; 3) polimorfismo complejo.

An alternative analysis can be based on criteria that can be presumed to have been selected in response to predation (Figure 4). Two alternatives are available as anti-predator responses : avoidance or resistance. Each strategy dictates particular suites of structural and behavioral traits.

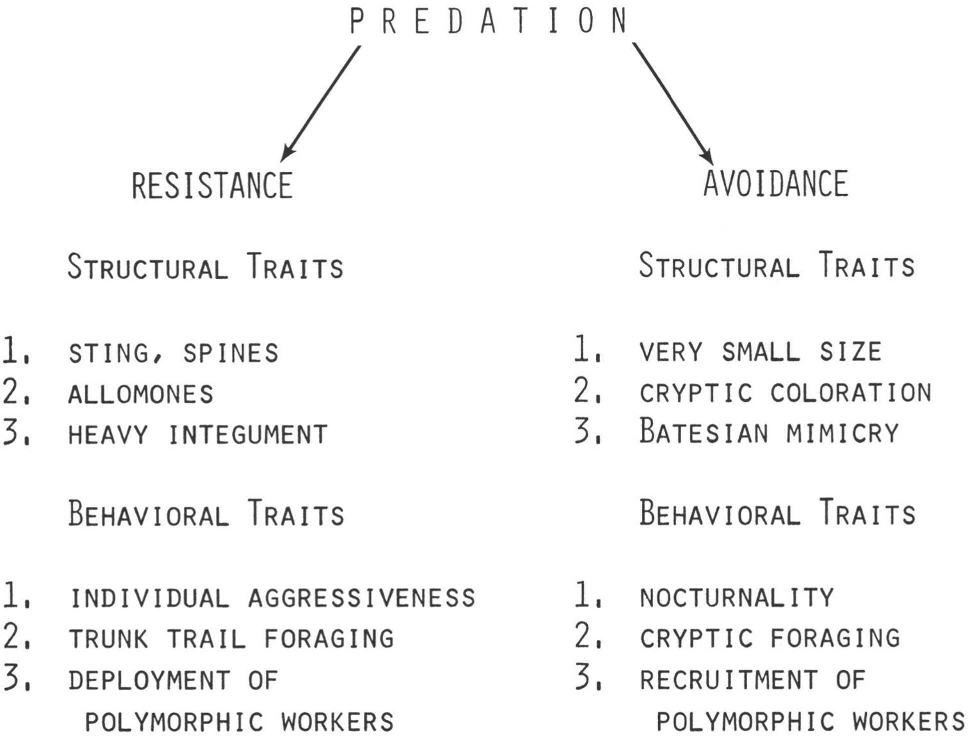

Fig. 4 – Ants subjected to vertebrate predation may have adopted strategies of either resistance or avoidance. Examples of morphological and behavioral traits corresponding to each strategy are listed.

Fig. 4 – Las hormigas expuestas a la predación de los Vertebrados pueden haber adoptado la estrategia de resistir o la de evitar. Estan apuntados ejemplos de carácteres morfológicos o de comportamiento correspondiendo a cada una de las dos entretegias.

By simultaneously considering both of these analyses some speculative propositions can be put forward. The striking absence of worker polymorphism in species that forage solitarily and have poor recruitment or none suggests that such species have few options vis a vis possible predation. One possibility is to resist predation through a combination of individual aggressiveness and a potent sting. Probable examples of this strategy include *Paraponera* in the neotropics, *Pachysma* in Africa, and *Myrmecia* in Australia. An alternative strategy is to avoid predators by cryptive foraging. Species of *Leptothorax* and small ponerine species that recruit via tandem running may exemplify this strategy. Two similar alternative strategies may also apply to legionary predators. Small species of *Neivamyrmex* may avoid predation by foraging cryptively or nocturnally ; larger species such as *Eciton* and *Dorylus* doubtless resist predators by virtue of aggressiveness and potent offensive weaponry. The presence of trunk trail foraging in legionary predators that follow both strategies strongly suggests that such trunk trails are more likely selected for as a resource acquisition strategy than as an anti-predator strategy. The conspicuous worker polymorphism in *Eciton* species seems more closely related to resources rather than to predators.

The largest variety of anti-predator strategies is restricted to two of the foraging ecology groups (Figure 3), solitary foragers with good worker recruitment and group foragers that take stationary resources. Large numbers of ants that are concentrated in a small area, whether by recruitment or by virtue of group foraging, would seem to offer a potentially substantial resource reward to a predator. It seems, then, that anti-predator strategies should be sought in these species even if such strategies are not as immediately apparent as are potent stinging and cryptiveness. One of the more apparent defenses found in these species is the use of repellent or distasteful chemicals. These chemicals, which can be called allomones, are conspicuous in some species. The dolichoderine *Liometopum occidentale* was the most abundant and conspicuous diurnal ant at one of the sites I studied in California (Hunt, 1973). These ants, in groups, produce a pungent aroma that is detectable by humans at distances of a meter or more. Single ants are extremely distasteful to me, and, I suggest, would also be so to any other vertebrate. Less pronounced but similar distastefulness is probably characteristic of most of the subfamily Dolichoderinae. Among myrmicines and formicines, *Crematogaster* and *Formica* exemplify taxa that are capable of exuding or even spraying repellent chemicals such as formic acid. In recent years extensive and excellent work has been done in a number of labs on the biochemistry and physiology of allomone defenses. In the present context, then, I want only to suggest what seem to me to be some foraging strategy correlates of allomone defense systems. These defenses, in my experience, seem limited to ant species that are small to medium in size, that forage in groups, and that lack both stings and worker polymorphism. Most such species seem to specialize on aphid honeydew or on nectar.

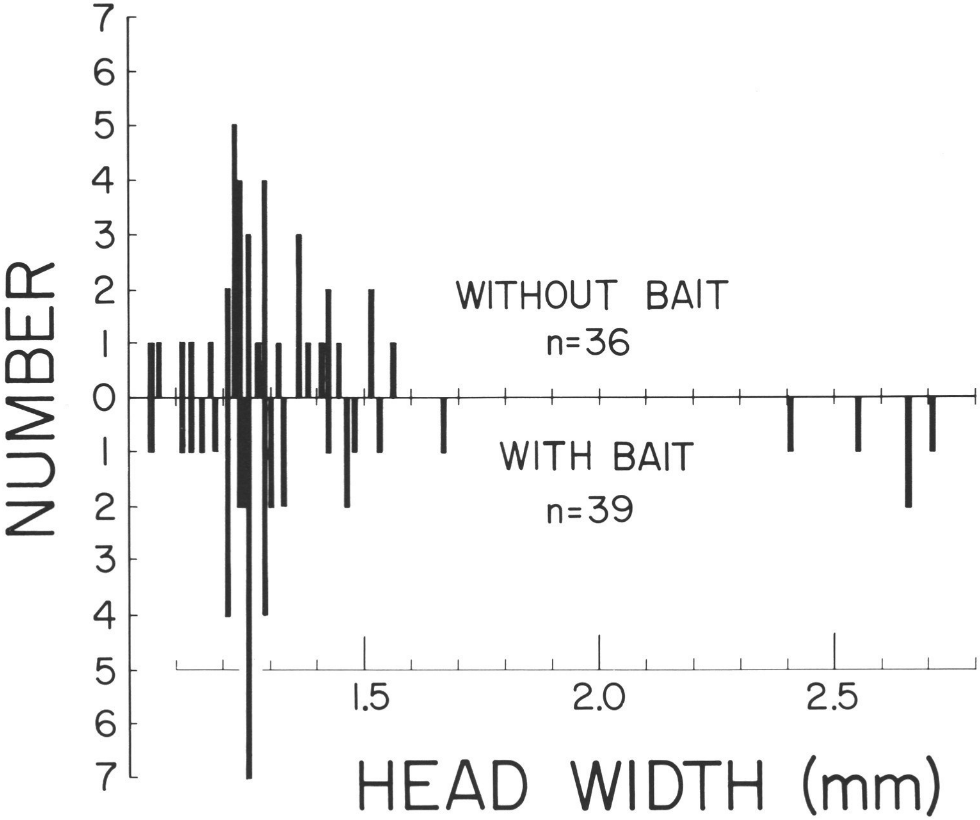

Fig. 5 – Frequency histograms of *Camponotus distinguendus* head widths for workers systematically sampled on two successive days. On the first day, without bait present, no major workers appeared ; on the second day, with bait present, five major workers were taken in the sample.

Fig. 5 – Histógramas de frecuencias de *Camponotus distinguendus* (anchura de la cabeza), siendo las obreras sistemáticamente colectadas durante dos días sucesivos. En el primer día, sin cebo, no aparecieron las obreras mayores ; el día siguente, con cebo, cinco obreras mayores fueron colectadas.

Species that do exhibit worker size polymorphism offer some of the most interesting anti-predator strategies. In Chile I sampled foragers exiting a nest of *Camponotus distinguendus* on two days, one when baits were deployed and one when they were not. Major workers foraged only on the day when baits were present (Figure 5). Carroll and Janzen (1973) cite corresponding results by a number of other investigators, and they suggest that the pattern of foraging by small workers and recruitment of larger workers is in part to minimize the cost per searcher. However, the cost being minimized is not energetic cost of foraging, as reading of Carroll and Janzen might suggest, for equal search areas are doubtless covered with greater energetic efficiency by larger workers. I suggest that the cost being minimized is cost to the colony of loss of a forager to predation. Larger workers that are energetically more expensive to produce are placed at risk only when the probable resource reward merits that risk. I believe that many allometric or polymorphic species in genera such as *Pheidole* and *Camponotus* use this strategy, which I refer to as recruitment of polymorphic workers (Figure 4). This strategy can both optimize resource aquisition and minimize possible loss to predation.

An alternative strategy is employed by *Atta cephalotes. A. cephalotes* is a strongly polymorphic leaf cutter ant that forages using conspicuous trunk trails. The species lacks a sting and is not distasteful, yet it seems to enjoy a puzzling immunity to predation. I suggest that Henry Walter Bates (1892) very nearly correctly assessed the strategy employed when he identified the large major workers as playing a passive defensive role. These large major workers do not cut or transport leaves nor do they work inside the nest. They have, however, sharp mandibles capable of delivering a powerful scissors-like bite (Figure 6). It seems likely to me that a naive predator that ingested such an ant would most likely sustain injury to its mouthparts or gullet. That predator might then well remember the encounter and so avoid any similar future predation attempts. Close-association of the major workers with the foraging workers could then engender an immunity to predation for all. I have referred to this strategy as deployment of polymorphic workers (Figure 4). Other species that deploy major workers, such as *Solenopsis saevissima* (Wilson, 1971), may well be exploiting this strategy.

The trunk trail foraging by *A. cephalotes* may well have been selected for in part, if not primarily, by virtue of its anti-predator value. Working foragers are conspicuously and closely associated with the defensive majors that accompany them. What, then, can be the selective basis for trunk trail foraging in monomorphic species ? The *Pogonomyrmex* species that I discussed at the beginning of this paper include two species that forage using trunk trails. Though a resource based selective mechanism can be argued, I have suggested predation as an alternative. Some anecdotal observations are thus noteworthy. Lizards of the genus *Phrynosoma* are specialist ant eaters that emphasize *Pogonomyrmex* in their diet. R.R. Snelling (personal communication) offered 10 or 12 *Pogonomyrmex californicus* as food to captive *Phrynosoma*, and on two occasions the ants swarmed over the lizards, biting and stinging them. One of the lizards subsequently stopped eating and died of starvation ; the other lizard continued to eat *Formica, Myrmecocystus*, and

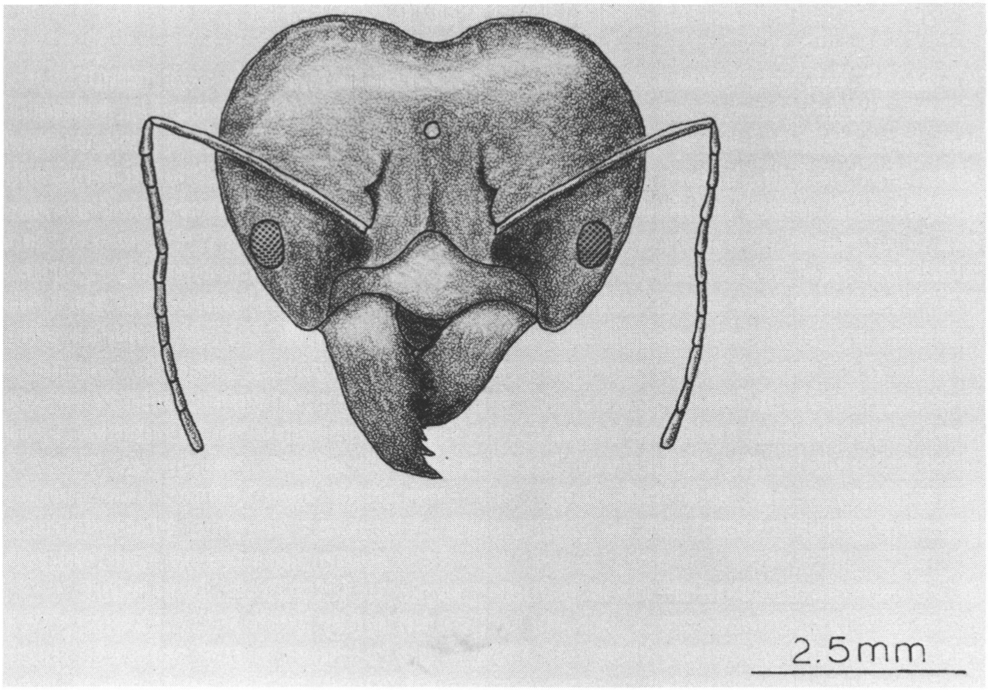

Fig. 6 – An *Atta cephalotes* major worker showing the scissor-like mandibles.

Fig. 6 – Una obrera mayor de *Atta cephalotes* enseñando sus mandíbulas en forma de cizalla.

other ants, but it retreated from all *Pogonomyrmex* and majors (but not smaller workers) of *Solenopsis xyloni*, which somewhat resemble *Pogonomyrmex*. I would expect, then, that *Phrynosoma* in natural situations take primarily isolated foragers of *Pogonomyrmex* either at the sides or terminus of trunk trails. Predation directly upon ants massed in a group could well result in a situation as Snelling observed in captivity. Trunk trail foraging in *Pogonomyrmex* may well have been selected for in those species that can resist predators only en masse. The solitary foraging *P. maricopa* may well be able to resist predators on an individual basis.

At this point I would like to turn to a single brief field study that presents data relevant to my speculations. During February 1-4, 1974, I collected foraging ants at Barro Colorado Island, Panama, in a manner as much like a lizard or anuran as I could conceive. I spent periods of time two hours or longer in the forest each morning, afternoon, and night. I sat motionless for long periods or moved slowly about and collected all foraging ants that I could procure. I made no attemps to disturb leaf litter, displace vegetation, etc. in searching for ants. I simply collected what I saw as I saw it. Sixty-six species were collected in this manner. The ants were collected into 70 % ethanol, and about 3 months later I removed the ants, air dried them on filter paper for five minutes, and then weighed them. The array of ant sizes, by subfamily (Figure 7), shows some noteworthy patterns.

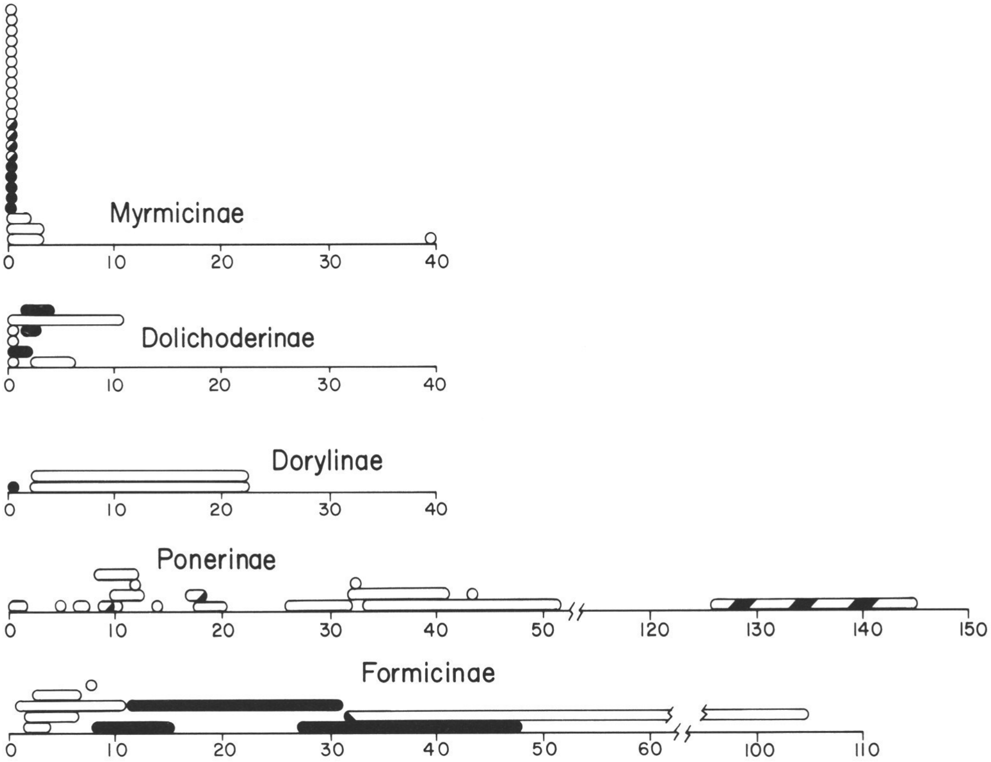

Fig. 7 – Array of weights of worker ants, by subfamily, as collected at Barro Colorado Island, Panama. Ant weights are given on the horizontal axis in milligrams. Each circle or bar represents a single species ; a circle represents either a single specimen or multiple specimens of the same weight ; a bar spans the range of weights for collected individuals of a species. Open figures (o) indicate species collected only by day ; closed figures (●) indicate species collected only at night ; partially shaded figures (o) indicate species collected both day and night.

Fig. 7 – Clasificaci*ó*n, por pesos, de la hormigas obreras colectadas en la isla de Barro Colorado, Panama. Los pesos estan dados en milígramos (eje horizontal), cada círculo o barro representa una sola especie ; un círculo puede representar un solo individuo o varios del mismo peso ; une barra representa la distribución de los pesos en los individuos colectados de una especie. Las figuras en blanco (o) indican las especies colectadas en el día ; la oscruras (●) las colectadas en la noche ; las figuras rayadas (o) indican las especies que se encontraron de día y noche.

All myrmicine foragers but one were small to very small. Many of these species, notably the 11 *Pheidole* species, doubtless have larger workers than were encountered in this sampling. That only small workers were encountered suggests that these ants may employ a recruitment of polymorphic workers strategy and so generally avoid predation. The one large myrmicine encountered, *Cephalotes atratus*, is arboreal, has a very heavy integument, and is conspicuously spinescent (Figure 8) , all of these characters suggest a strategy of resistance to predation.

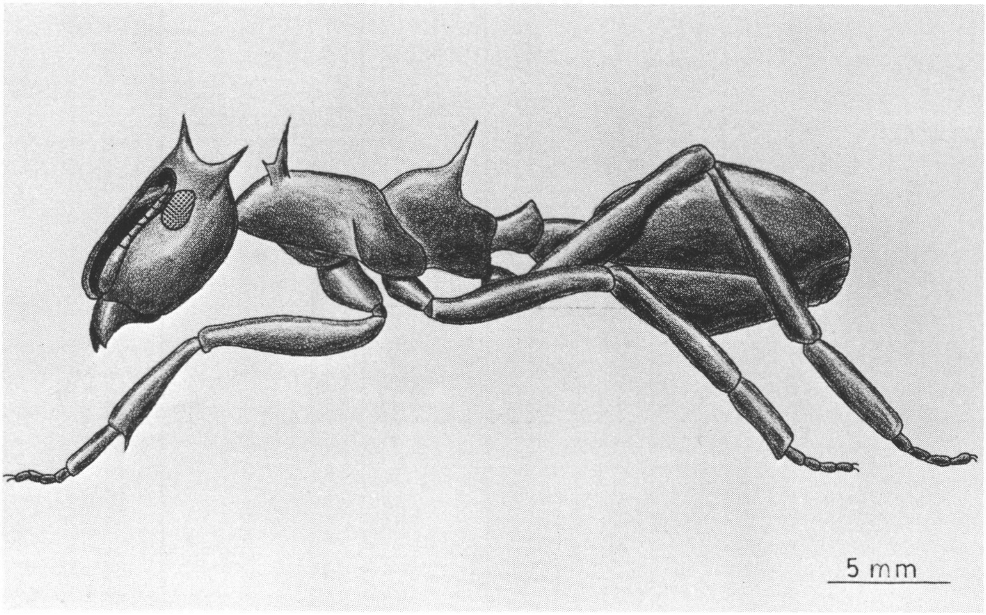

Fig. 8 – A *Cephalotes atratus* forager

Fig. 8 – Una abastecedora de *Cephalotes atratus*

The dolichoderines, which I suggest may be predator resistant by means of allomones, were small to medium in size. Most of the species were found conspicuously foraging in large numbers. The one small doryline encountered was nocturnal. The two *Eciton* species are small to medium sized and are probably resistant to predation by virtue of aggressiveness and sting potency. The ponerine species were medium to large in size, and on three painful occasions in this sampling I was reminded of the potent stinging ability of larger ponerines. The largest species encountered in this sampling, *Paraponera clavata*, is a solitary forager whose sting is held in high regard by all who work in the neotropical lowland forests (Figure 9). *Paraponera* is a conspicuous ant as it forages, and it responds aggressively to attempted capture.

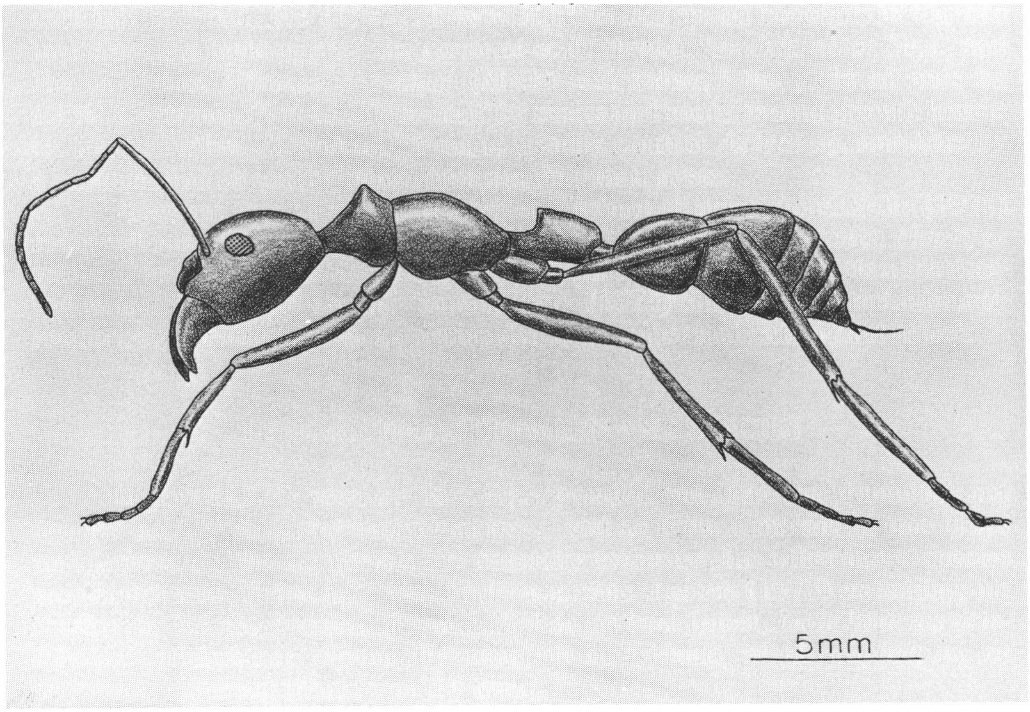

Fig. 9 – A *Paraponera clavata* forager.

Fig. 9 – Una abastecedora de *Paraponera clavata*

The formicines offer some of the most varied patterns. The foragers ranged from small to large. The small diurnal species were largely to exclusively arboreal and so may avoid many predators. The largest species, *Camponotus sericeiventris*, forages both terrestrially and on tree trunks and larger branches, both diurnally and nocturnally. Large workers are seen foraging individually and moving slowly about ; they are characterized by a heavy integument, large head, and powerful mandibles (Figure 10). The other large

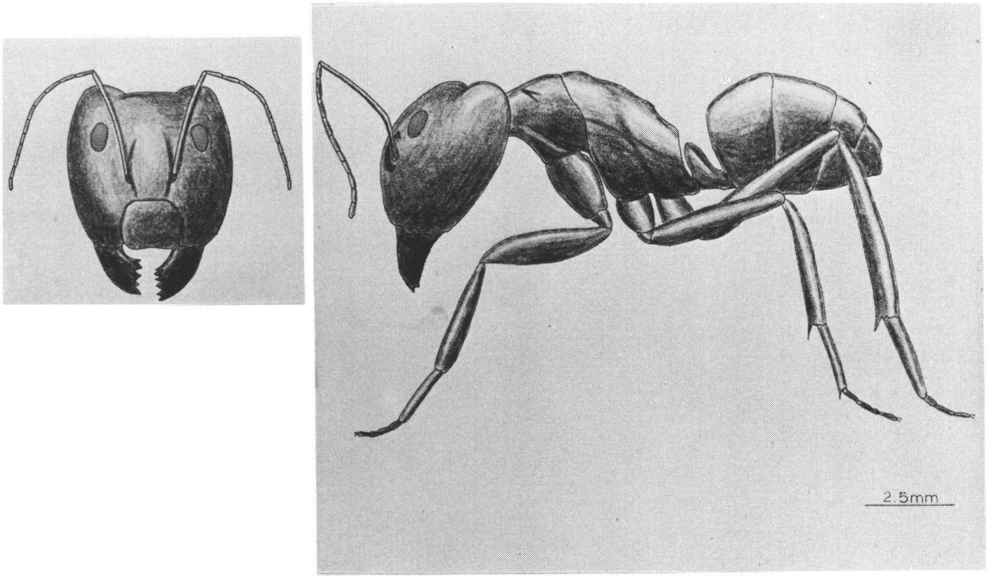

Fig. 10 – A large worker of *Camponotus sericeiventris* collected foraging by day.

Fig. 10 – Una obrera grande de *Camponotus sericeiventris*, colectada forajeando en el día.

formicines are nocturnal. The largest of these, *Camponotus agra*, is typical in having long legs and rapid movement, a soft integument, and a small head with mandibles that are ineffectual in biting (Figure 11). This suite of characters suggests predator avoidance. To me, these patterns in formicinae and those for the other subfamilies all conform to the proposition that is the basis of this paper, that predation by vertebrates has exerted strong selective pressure on morphology and foraging ecology in these ants.

Lastly, let me note that of course there will be exceptions to the generalities I have presented. In some cases, however, these may be the exceptions that prove the rule. Two examples will suffice. In my California studies I noted that species of *Veromessor* harvester ants forage diurnally in conspicuous trunk trails, yet they lack stings, polymorphic workers, and, apparently, allomones. They possess, however, a strong resemblance to *Pogonomyrmex* species. I suggest that they may exploit a mimetic similarity to *Pogonomyrmex*, and I believe, though data are lacking, that they emphasize critical components of the trunk trail strategy : they are more tightly

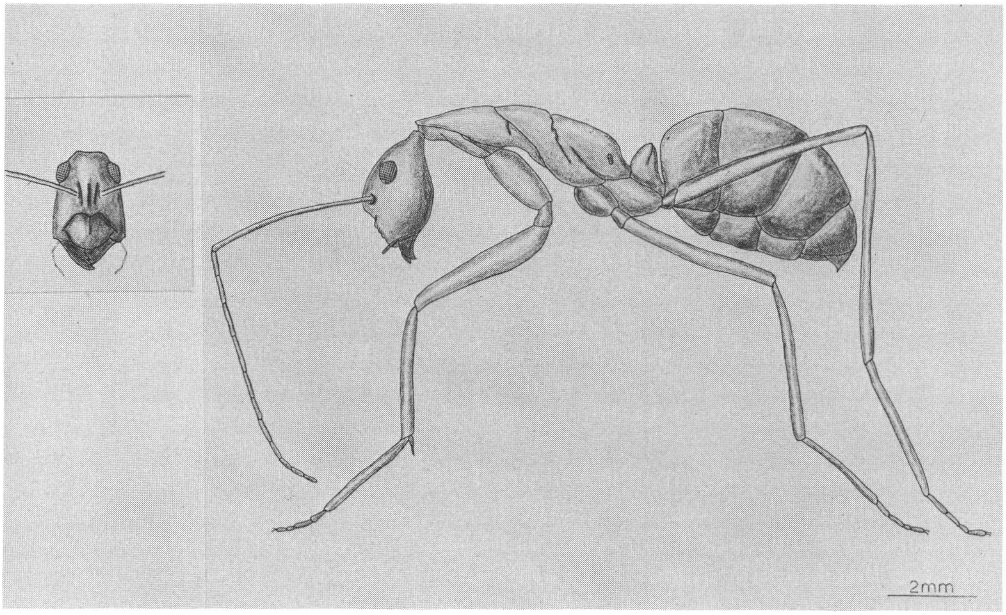

Fig 11 – *Camponotus agra*, a large nocturnal formicine.

Fig. 11 – *Camponotus agra*, una formicina noctuna grande.

massed in the trail and so are generally more conspicuous than are *Pogonomyrmex* ; fewer foragers stray to the sides of the column ; and the foraging fan at the terminus of the column is smaller than in *Pogonomyrmex*. As with all good Batesian mimics, they thus scrupulously minimize the possibility that a predator might discover the ruse. My second exception is from the Amazonian lowlands near Iquitos, Peru. There I chanced upon a diurnal, terrestrial, medium-sized, individual ant that was clearly a formicine. I was immediately struck by this ant as foraging in a manner counter to all my preconceptions based on predation. I watched this ant with great curiosity for several minutes before attempting to collect it, and as I did so I was thoroughly surprised. As I reached for the ant it jumped ! The ant jumped quickly and repeatedly, for distances up to 5 cm, and it successfully evaded capture for a frantic half minute or longer. The species, *Gigantiops destructor*, has the largest eyes in relation to its size of any new world ant known to me (Figure 12). Its unique traits of morphology and behavior seem clearly selected for by vertebrate predation.

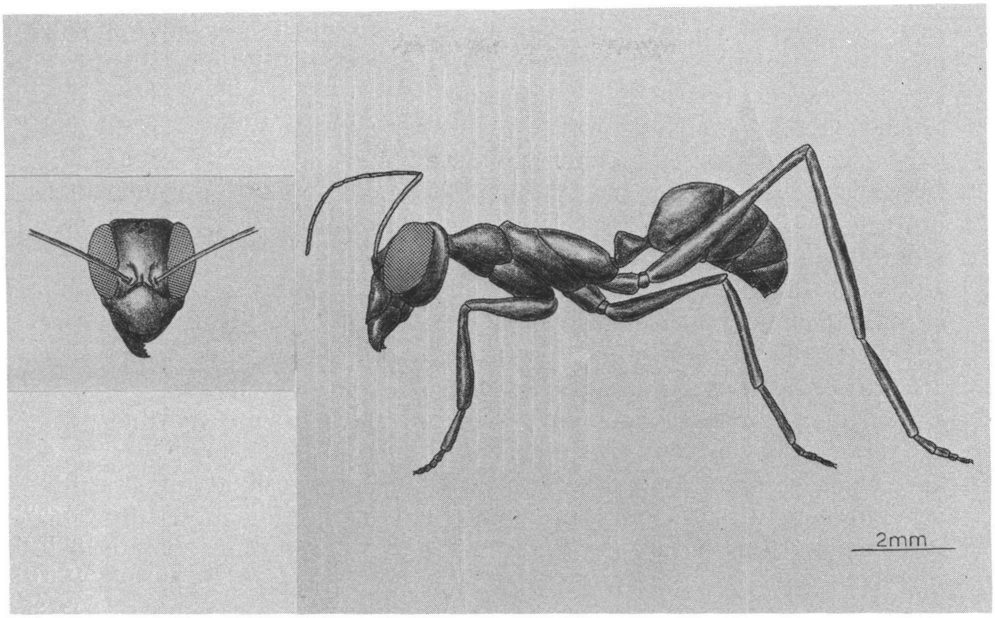

Fig. 12 – *Gigantiops destructor*, a diurnal, terrestrial, solitary foraging formicine from the Amazon lowlands.

Fig. 12 – *Gigantiops destructor*, una formicina de tierras bajas de Amazonas, diurna, terrestre y forajeando sola.

CONCLUSION

In conclusion, I have taken the opportunity provided by this symposium to offer some admittedly speculative ideas on a proposed relation between the foraging and morphology of ants and the role of ant eating vertebrates, notably lizards and anurans, as agents of selection. Many of the ideas I have presented are doubtless not original, and I have probably transgressed on the work of other reserachers. The meagre data I have presented are merely suggestive. I have tried to indicate, however, my conviction that a pattern of varied but coherent responses to vertebrate predation exists in the foraging ecology of ants.

A non-exclusive listing of relevant traits as I see them includes the following :

1 – Species that forage solitarily and have poor recruitment or none also lack worker polymorphism. Such species may either resist predation via large size, aggressiveness, and weaponry ; or they may avoid predation via cryptiveness, nocturnality, or small size.

2 – Small legionary predators forage cryptively or nocturnally ; larger legionary predators are aggressive and have potent weaponry. Trunk trail foraging in these species may be more strongly related to resource aquisition than to predator resistance. Polymorphism in army ant workers seems resource related.

3 – Allomone defense systems are generally found in ants small to medium in size that are monomorphic, that frequently have a soft integument, and that generally forage in groups. Ants with allomone defense systems are frequently conspicuous aphid pastoralists or nectar gatherers.

4 – Ants that are generally defenseless against predators but that have good recruitment may employ a recruitment of polymorphic workers strategy.

5 – Species in which major worker can serve a defensive function may exhibit a deployment of polymorphic workers strategy. Trunk trail foraging in such species may have been selected for as an important component of this strategy.

6 – Trunk trail foraging may also be found in species that can resist or repel predators but only successfully do so when in groups.

7 – Mimicry, both Batesian and Mullerian, seems possible among ants. In this regard the well known ant mimicry among many families of non-ant insects and of spiders seems to call for particular study of the anti-predator defense system of the ant models themselves.

In conclusion, I have tried to indicate in this paper that full consideration of these responses to predation can add perspective and significance to resource centered analyses of foraging strategies in ants. I will close, then, with my personal conviction : when studying the foraging ecology of ants, especially in the tropics, one should assume a major selective role for vertebrates until the data demonstrate otherwise.

ACKNOWLEDGMENTS – I thank Bernice Bacon DeMarco for the excellent ant illustrations plus several of the other figures that accompany the text. Joyce Henderson was of considerable assistance in preparing the manuscript ; Kathleen Metter Kohl also helped. I also thank Zuleyma Halpin for translating the Spanish summary. The field work discussed in the text was supported by U.S. NSF grants #'s GB 31195 and GB 27148 as part of the Structure of Ecosystems Subprogram of the International Biological Program. During manuscript preparation the author was supported by U.S. NSF grant # DEB 7904192. I especially want to thank Jane and Noah for their patience and support.

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Appendix A : Ants collected at Barro Colorado Island, Panama
February 1-4, 1974

	When collected*	Size (mg)
Subfamily Ponerinae		
Paraponera clavata	ND	128.6-145.9
Ectatomma ruidum	D	8.7-10.1
Ectatomma tuberculatum	N	14.1
Pachycondyla apicalis	D	27.1-32.2
Pachycondyla carinulata	D	6.3
Pachycondyla harpax	D	10.3-12.0
Pachycondyla impressa	D	34.4-52.2
Pachycondyla laevigata	D	12.0
Pachycondyla obscuricornis	D	17.0-19.4
Pachycondyla striatiodis	D	8.8-11.4
Pachycondyla velosa	D	45.1
Anochetus inermis	D	1.1
Odontomachus chelifer	ND	33.3-41.0
Odontomachus haematodus	ND	16.3-17.4
Odontomachus minutus	N	4.2-4.8
Subfamily Dorylinae		
Eciton burchelli	D	1.8-25.0
Eciton hamatum	D	2.3-23.8
Neivamyrmex sp.	N	0.3-1.0
Subfamily Pseudomyrmecinae		
Pseudomyrmex sp. A	D	2.0-2.5
Pseudomyrmex sp. B	D	0.9
Subfamily Myrmicinae		
Aphaenogaster sp.	D	0.9
Pheidole sp. A	D	0.1-0.3
Pheidole sp. B	D	0.3

*N : night – D : day

	When collected	Size (mg)
Pheidole sp. C	N	0.2
Pheidole sp. E	N	0.3
Pheidole sp. F	D	0.1
Pheidole sp. G	N	0.3
Pheidole sp. H	D	0.3
Pheidole sp. I	D	0.3
Pheidole sp. J	N	0.3
Pheidole sp. K	ND	0.1-0.4
Pheidole sp. L	ND	0.2-0.3
Crematogaster sp. A	D	0.3
Crematogaster sp. B	N	0.4
Solenopsis sp. A	D	0.2
Solenopsis sp. B	D	0.2
Ochetomyrmex auropunctata	ND	0.1-0.3
Cephalotes atratus	D	39.3
Paracryptocerus multispinosus	D	0.4-0.9
Sericomyrmex amabilis	D	0.7-0.9
Apterostigma mayri	D	0.6
Cyphomyrmex rimosus	ND	0.3
Cyphomyrmex salvini	D	0.9
Trachymyrmex morgani	D	0.8-1.2
Trachymyrmex sp. A	N	2.8
Trachymyrmex sp. B	D	0.9
Trachymyrmex sp. C	D	2.0
Subfamily Dolichoderinae		
Dolichoderus laminatus	ND	2.4-5.0
Azteca sp. A	N	0.7-1.3
Azteca sp. B	D	0.4-0.9
Azteca sp. C	D	0.3
Azteca sp. D	N	0.6
Azteca sp. E	N	1.2-2.4
Azteca sp. E	D	0.3-10.9
Azteca sp. G	N	1.0-3.4
Subfamily Formicinae		
Camponotus abdominalis	N	7.7-14.5

	When collected	Size (mg)
Camponotus agra	N	27.0-47.0
Camponotus brettesi	D	1.0-2.0
Camponotus brevis	D	1.1-5.4
Camponotus lindigi	D	0.3-10.9
Camponotus sericeiventris	ND	31.1-105.5
Camponotus simillimus	N	11.0-29.5
Camponotus zoc	D	2.3-5.6
Dendromyrmex chartifex	N	7.3

INTERSPECIFIC TROPHALLAXIS IN ANTS, ITS ECOLOGICAL AND EVOLUTIONARY SIGNIFICANCE

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SUMMARY

Interspecific trophallaxis or ingluvial liquid food exchange between certain species of ants is prevalent at intergeneric and intertribal level in neotropical and nearctic Myrmicinae and palearctic Formicinae. Radiotracer studies on the workers and reproductives of *Formica, Lasius* and *Camponotus* species in Central Europe and observations on the confrontation behavior of *Solenopsis invicta, S. geminata, Pheidole dentata* and *P. morrisi* at the methylene blue-dyed sucrose baits in the fire regenerated habitats in Florida brought out the occurrence of food exchange between their colony members. This behavior may indicate the coadaptation in ants, regardless of their nesting in similar or distinctly different habitats or geographical regions, should certain species confront one another. The evolutionary significance of interspecific trophallaxis in relation to social symbioses is discussed.

ZUSAMMENFASSUNG

Interspezifische Trophallaxis bei Ameisen, ihre ökologische und entwicklungsgeschichtliche Bedeutung

Interspezifische Trophallaxis oder Austausch von flüssigem Kropfinhalt zwischen bestimmten Arten, Gattungen und Tribus von Ameisen ist weit verbreitet bei gewissen

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neotropischen und nearktischen Myrmicinae sowie palearktischen Formicinae. Untersuchungen mit radioaktiven Markierungssubstanzen an Arbeiterinnen und Geschlechtstieren von *Formica, Lasius* und *Camponotus* Arten Zentraleuropas und Beobachtungen des Konfrontationsverhaltens von *Solenopsis invicta, S. geminata, Pheidole dentata* und *P. morrisi* an Methylenblau gefärbten Sucrose-Ködern in feuer-regenerierten Habitaten Floridas ergaben eine interspezifische Trophallaxis zwischen den Mitgliedern ihrer Kolonien. Sollten sich gewisse Arten einander begegnen, so läßt dieses Verhalten auf eine Koadaptation bei Ameisen schließen, ungeachtet ihres Vorkommens in gleichen oder völlig unterschiedlichen Lebensräumen und ihrer geographischen Verbreitung. Die entwicklungsgeschichtliche Bedeutung der interspezifischen Trophallaxis bezüglich sozialer Symbiosen wird diskutiert.

INTRODUCTION

Ingluvial exchange of food beyond a colony or species level, especially in non-symbiotic species of ants, has not received enough attention. Stray observations by earlier workers neither document the phenomenon per se nor include the behavioral repertory of the species in question. Kutter (1964) noted food exchange between *Lasius fuliginosus* and several species of *Formica (exsecta, fusca, truncorum, rufa, pratensis)* by interconnecting their colonies to form so called «alliance» colonies in an arena. Gösswald and Kloft (1960) observed the transfer of radioactivity from *L. niger* to *L. flavus* workers when the former carried ^{32}P mixed honey water. Bhatkar (1973) documented a delay in colony invasion when *Solenopsis invicta* was confronted to the food carrying workers of *Pheidole dentata* or *P. morrisi.* Near the nest entrance these latter species offered food to *S. invicta*, and the major workers received more food than the minors when any one of these species was a donor (Bhatkar and Kloft, 1977). Among symbiotic species, the dulotic species seem to be dependent on their hosts for feeding, and less so the temporarily parasitic species (Gösswald and Kloft, 1960 ; Beck, 1961). Interspecific food exchange seems to be occasional in xenobiotic species, such as *Formicoxenus nitidulus* and *Formica* spp. (Wheeler, 1910 ; Stumper, 1950), and parabiotic species, such as *Camponotus femoratus* and *Crematogaster limata parabiotica* (Wheeler, 1921 ; Swain, 1980). Here, I report the prevalence of interspecific food exchange beyond specific, generic and tribal level in the subfamilies Formicinae and Myrmicinae, with special reference to non-symbiotic species, occurring in ecologically similar and distinct habitats and discuss the evolutionary significance of the phenomenon. Comparative investigations on the members of two major subfamilies of ants in two geographical areas are discussed below.

MATERIALS AND METHODS

The comparative investigations involved two sites, the Tall Timbers Research Station, Tallahassee, Florida during 1973-75 and the Institute of Applied Zoology, Bonn during 1975-1977. The ants involved contained neotropical and nearctic species in Florida and palearctic species in Central Europe. The direct observations were given more weight over supplementary quantitative data on indirect observations.

Baiting experiments

Annually burned, regenerated, 0.2 hectare square plots, containing some tall trees and annual vegetation in North Florida, were baited along their diagonals at 5 m distant 10 sites. For this, cotton wicks, about 3 cm in length and 0.5 cm in diam (Dispo, Scientific Products, Illinois), were soaked in 20 % sucrose solution and placed individually at the bottom of the 17 x 7.5 cm wire-rimmed Whirl Pak (Nasco) plastic bags. The aqueous sucrose solution contained 5 % methylene blue as a tracer and it could be seen in the fed ants and in the ants that acquired food secondarily from the fed ants by squashing them on pieces of blotting paper. The bags were laid horizontal with their wired rims separated open and observations were made by periodically walking from each bait site for about 6 h. Three such 150-200 m distant plots were baited at the study site. Once the ants of one species recruited to food, close behavioral observations on the next species recruited continued at the same site. The wick was now separated from the 2nd species in the bag by placing a heavy metal rod beside the wick but over the bag. This seemed not to markedly change their behavior. Usually several cases of food transfer between the species in contest occurred within first 20 min. After this the ants were immediately killed with chloroform, and bags were sealed by pulling the wires close and folding three times. Only the ants in the front one-half of the bag were sampled by squashing.

Colony confrontation experiments

A vertical, centrally partitioned, 40 cm wide, 30 cm high double plastic sheet-nest was used for these studies. It provided 17 x 29 x 0.4 cm nesting space for each of the two species. The top of the nest was sprayed with Fluon (ICI America) to prevent ant escape. The bottom was perforated and held under water up to 4 mm so that the soil within the nest absorbed moisture. Two partitions of the nest could be connected to the ant colonies, reared in 20 cm diam, 3 cm high (18 cm diam, 1 cm high, inner dimensions) Wilson cells (Wilson, 1962) in soil-free conditions. *S. geminata, S. invicta, P. dentata* and *P. morrisi* thus raised excavated the soil in preference to soil-free condition and moved in. An apical 4 cm piece of the partition was then removed and the confrontation behavior between *S. invicta* and other species observed. Also, the colonies in the Wilson cells themselves could be connected through a 40 cm long, 0.5 cm diam glass tubing, centrally provided with a two-way stopcock, and the colony confrontations observed under completely soil-free conditions. The details of collecting colonies under soil-free conditions are discussed in Bhatkar and Whitcomb (1982).

The boreomontane species, such as *F. lugubris, F. aquilonia,* and *F. exsecta* were obtained from the Austrian Alpine National Park, Königssee. Other formicine species were collected from various areas in Germany : *F. polyctena, F. pratensis, F. fusca* and *F. sanguinea* from Steinerberg, Eifel ; *F. rufa* (monogynous form) from Krebssee, Kitzingen ; *F. rufa* (polygynous form) from Reupelsdorf in Franconia ; *Camponotus ligniperda* from Landesacker near Würzburg, and *L. niger* from Kottenforst near Bonn. All these species were reared in 30 cm square plastic boxes, 10 cm wide, in their own nesting material and fed on artificial diet, supplemented with some insect and fruit tissue (Bhatkar and Whitcomb, 1970). The nests were connected to two 10 cm diam, 5 cm high plastic dishes, which could be interconnected through a 30 cm long, 1 cm diam glass tubing with a two-way stopcock. The bottoms of the dishes were provided with a fine screen and they could be mounted on similar such dishes containing certain saturated salt solutions (Winston and Bates, 1960), to hold 60 % RH at $25 \pm 2^\circ$ C. Any two species of ants were allowed to collect in the upper dishes and the passage between them was opened.

Radioisotope experiments

A procedure similar to that for myrmicine species (Bhatkar and Kloft, 1977 ; Bhatkar, 1979) was used for the formicine species, except that larger confrontation cages were constructed using 2.5 cm diam, 2.5 cm wide plastic ring, hinged together to a similar 1 cm wide piece with sealing tape. The top ring was provided with a fine screen (material of lady's single-knit stockings, Fig. 1) to prevent ant escape and to avoid accumulation of formic acid that is otherwise autocidal to the secreting ants. About 50 foraging ants were fed to satiation with 20 % aqueous sucrose and $H_3{}^{32}PO_4$ (sp. act. 7.4 MBq ml^{-1}) mixture in 10 cm diam, 5 cm wide glass dishes. They were surface decontaminated by passing through plain water, 3 % NaH_2PO_4 solution and plain water by holding them in the middle with fine watch spring forceps and blotting on a tissue paper. As a test of decontamination externally decontaminated dead ants were used in control. The efficiency of a similar procedure is discussed in Kloft et al. (1976). Individual ants were held in uniformly horizontal position in 0.7 cm pieces of clear plastic tubing, slightly larger in diam than the ant's length, and placed on 1 cm aluminum discs. The tops of the enclosures had a fine screen mentioned above. The radioactivity of live ants was measured with GM-end-window (thickness 1.2-1.4 mg cm^{-2}) counting tube in conjunction with Philips Scaler Timer, Printer and Automatic Sample Changer. First, a satiated (with high radioactivity) worker or reproductive of one species and then 4 unfed workers or reproductives of another species were inserted in the confrontation cage by slightly tilting its top ring. Behavior of the contestants was observed under a stereoscope and they could be simultaneously

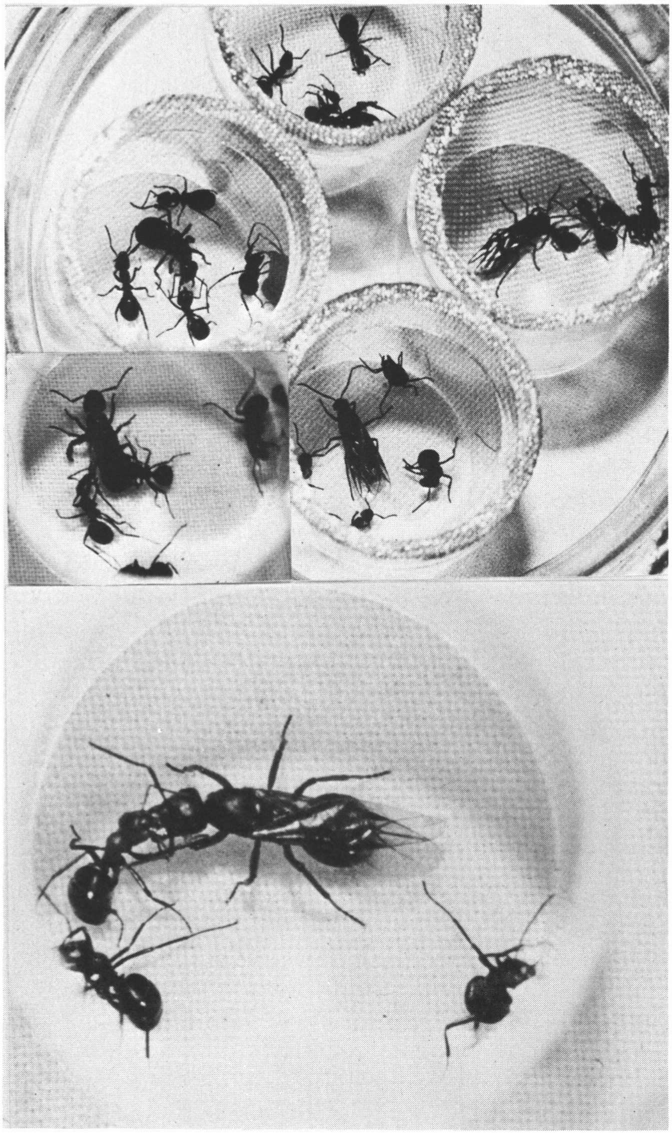

Fig. 1 – Interspecific food exchange between the alate queens of *Formica pratensis* and workers of *F. polyctena*. The queens offered food in response to aggression from workers (queen with malformed wings) and grooming followed such food offering.

Abb. 1 – Interspezifischer Futteraustausch zwischen geflügelten Königinnen von *Formica pratensis* und Arbeiterinnen von *F. polyctena*. Die Königinnen erwiderten das aggressive Verhalten der artfremden Arbeiterinnen mit Futterabgabe, der eine Säuberung folgte (Königin mit Mißbildungen der Flügel).

photographed. The ants were killed after a 20-60 min exposure, surface decontaminated and measured for acquisition of radioactivity through food exchange. The merits and general details of using radioisotopes in food exchange studies can be found elsewhere (Gösswald and Kloft, 1958 ; IAEA, 1977).

RESULTS

Baiting experiments

The experimental plots W1A, W1B and W1C have been burned during February-March annually since 1959 for a long duration floral and faunal succession study. Records indicate that the burns were carried out at 10-24° C and 30-72 % RH with a thorough back fire (fire backing into the wind direction) at 1400 h. The resultant vegetation included such regenerated trees as *Pinus echinata* (W1A, B), *P. taeda* (W1A, B, C), *Quercus virginiana, Q. nigra, Q. falcata* (W1B), *Q. velutina* (W1C), *Carya* spp. (W1A), *Liquidambar styraciflua* (W1A, C), *Nyssa silvatica* (W1B) and such annuals as *Cassia fasciculata, C. nictitans, Eupatorium* spp., *Solidago* spp., *Richardia scabra, Digitaria* spp. and *Paspalum* spp. Honeydew producing Homoptera, floral and extra-floral nectaries and insects provided a major diet for over 30 species of ants year-round. Only 13 species nesting in bare clay-loam spots predominantly exploited the baits. According to the degree of finding the baits and the persistance at feeding on them against the contestants, the species were divided into 1st degree, 2nd degree and 3rd degree recruiters.

Rapidly moving dolichoderine *Conomyrma flavopecta, Iridomyrmex pruinosum* and formicine *Camponotus floridanus, Paratrechina* spp., reached to the baits first, within 1/2 h of their placement. *P. dentata, P. morrisi* (nesting in the cultivated fire breaks around the plots), *S. geminata* and *S. invicta* first scouted the baits and recruited their workers within 2-4 h. They displayed alarm responses (rapid movement on antennal contact with the alien, opening mandibles, raising gaster and secreting venom droplets at the sting) towards the 1st degree recruiters already present. On attack by seizing appandages of the stingless dolichoderine and formicine species, the 2nd degree recruiters quickly dominated while the former disappeared and moved to yet undiscovered baits. A third group of tiny, 2-2.5 mm long ants, *Diplorhoptrum (S.) texana, D. pergandei, P. metallescens, Brachymyrmex* spp., recruited to the baits the last and fed simultaneously with the 2nd degree recruiters, keeping a 2-5 mm distance from them. They moved among them and slipped through their mandibles on attack. The 3rd and 1st degree recruiters never offered food to the aggressive 2nd degree recruiters, what the species of 2nd degree recruiters appeared to do, should *S. invicta* or *geminata* reach the bait and gradually replace them in contest. Whenever *P. dentata, P. morrisi* or *S. geminata* recruited to the baits prior to *S. invicta* by laying trails, the latter species elicited aggression by raising gaster, secreting a venom droplet at the sting, vibrating (stridulating) the gaster, opening mandibles and gradually moving towards the bait. They attacked (seized, severed, stinged) the aliens still approaching the bait. The alien food carrying workers moved slowly, oriented their heads to the aggressive *S. invicta* or *S. geminata* as the case may be, opened mandibles and regurgitated a droplet of fluid, pointing it to the attacker. The number of the two species of workers varied between 200-500 during the 20 min observation period and of these 50-80 % contained methylene blue (were potential donors) in the case of *P. dentata, P. morrisi* or *S. geminata*. The proportion of aggressive food recipients (*S. invicta* or *S. geminata*) was 8-10 times lesser than that of the donors (Table I). The food receiving workers elicited a diminished aggression by holding their mandibles open or seizing the legs of the food carrying aliens, groomed themselves or exchanged food with the sister workers. To observe the extent of this repertory, both the species in contest were separated from the food bait per se (see Materials and Methods). *P. morrisi* usually recruited to the bait sites towards the periphery of the plots and was not observed feeding together with *P. dentata*. Although *C. floridanus* and *Conomyrma flavopecta* nested close to the *S. invicta* and *geminata* mounds and fed on their dead workers, they never exchanged food. Whenever *S. invicta* recruited to the baits, it persisted the longest, displacing any other species that was its predecessor. However, the mortality of ants at the bait sites was less than 5 % of the total number recruited of any single species. Such contests were also observed at aphid-ant associations.

Table I – Proportion (%) of food donors and recipients containing methylene blue during the first 20 min of their confrontation. Summed data of 24 observations at 10 bait sites during September - November 1973-74 in 3 replicated plots.

Tabelle I – Verhältnis (%) von Futtergeber und Futterempfänger während der ersten 20 Minuten ihrer Konfrontation (als Nachweis dient Methylenblau). Zusammengefaßte Ergebnisse von 24 Beobachtungen an 10 Köderstellen in 3 Versuchsfeldern während September bis November 1973-74.

Donors	Recipients	Proportion of donors % ± SD	Proportion of recipients % ± SD
P. dentata	*S. invicta*	61.5 ± 15.4	5.6 ± 3.4
P. morrisi	*S. invicta*	72.3 ± 21.5	7.2 ± 3.2
P. dentata	*S. geminata*	59.3 ± 5.9	7.4 ± 3.2
P. morrisi	*S. geminata*	60.3 ± 15.9	6.8 ± 3.8
S. geminata	*S. invicta*	52.3 ± 14.3	4.2 ± 2.3
C. floridanus	*S. geminata*	80.7 ± 8.3	none

Colony confrontation experiments

An overt form of aggression was usually observed when the colonies of *P. dentata, P. morrisi, S. geminata* were confronted to those of *S. invicta*, or those of *S. geminata* were exposed to the attack of *Pheidole* spp. (Bhatkar, 1973 ; Wilson, 1976). The minor or major workers confronting first regressed to their own colonies and recruited a large number of major workers to the site near the entrance of *Pheidole* or *S. geminata* nests, as the case may be. The majors of *P. dentata* and *morrisi* were more aggressive than minors in these dimorphic species (attack responses by 100 majors of *P. dentata*, 61.2 ± 19.23 ; *P. morrisi*, 43.2 ± 7.63, $P < 0.05$; their minors, 14.2 ± 3.27 and 17.2 ± 9.12, respectively : replications 5), when exposed to equal numbers of *S. invicta* or *geminata* in Wilson cells. The attacks involved mandibular clasps, severing of legs, stinging by the species involved. When equal-sized colonies (1000 workers and a queen) of *P. dentata, P. morrisi* or *S. geminata* were confronted, *S. invicta* killed about 4 times its number of *Pheidole* spp. and twice its number of *S. geminata*, as a simple comparison. During 3-5 out of 10 confrontation studies, however, the food carrying workers of *P. dentata, P. morrisi* or *S. geminata* first opened their mandibles and alarmed the sister workers to the site of confrontation, and were also seen to regurgitate a droplet of fluid between their mandibles, orienting it towards an attacking alien. Initially, when the number of invading species was small, many workers accepted the regurgitate, redistributed it to the closest sister and groomed themselves, a repertoir that ceased colony invasions for 20-30 min. This behavior was also observed when an exodus of *S. invicta* workers entered the tunnels of these species and reached the queen and brood chambers. The chambers are usually inhabited by several major and few minor replete (with distended gasters) workers. These workers were still holding their antennae in repose, and upon encounters with an aggressive *S. invicta*, antennated it and offered food. The queen also took part in such a food exchange but the callow workers did not. The next response was swarming away from the site of attack by the queen, callows and rest of the workers, carrying the brood to deeper parts of the nest. Under laboratory conditions, the brood and the queen were stung and carried by *S. invicta* to its nest. In nature, the escape swarms by the attacked species may be successful. In fact, invasion by *S. invicta* of the colonies of *Pheidole* spp. and *S. geminata* was observed in the field in many instances and actual escape swarms occurred.

Formica rufa complex (*rufa, pratensis, polyctena, lugubris, aquilonia*) elicited aggression not beyond vigorous antennation, retreat, opening mandibles, alarming nestmates to the site of attack and pulling appandages of the alien workers when any two species were allowed to confront one another.

The workers mixed and exchanged food among themselves and with the aliens whenever the latter were aggressive. Over a 24 h period, more than 60 % of the mixed colonies again separated and they completely separated over a 3-5 days period. Concurrently, the interspecific food exchange was occasional. *F. exsecta, C. ligniperda* and *L. niger* colonies were the most aggressive towards *F. rufa* complex, and mandibular attacks, spraying of formic acid via acidopore, severing of appandages and heads were observed between the workers in contest. After 2-4 h initial aggression, the food carrying workers of *F. exsecta* and *C. ligniperda* appeared to offer the regurgitate to any alien worker in a fashion similar to the myrmicine species discussed above. However, *L. niger* workers apparently never offered food to any of these species. Trophallaxis also occurred between *C. ligniperda, F. pratensis, F. sanguinea,* and *F. fusca*. The members of *F. pratensis, F. fusca* and *F. sanguinea* mixed readily, albeit with initial aggression, when akinesis and food transfer were the means of suppressing aggression in the attacker. The recipients groomed themselves and the donors, contrary to the more aggressive myrmicine species. The queens of *fusca* and *pratensis* were invariably dead after a period of 20 days.

Radioisotope experiments

A certain degree of precision and quantification of the amount of regurgitate received as a proportion of the trophallactic uptake of the ingluvial fluids by the receiving species was possible through the use of ^{32}P. Since P is a part of the insect metabolism, it and low degree of radioactivity may not alter the behavior of ants (Gösswald and Kloft, 1960). The results of similar experiments on Myrmicinae using ^{32}P are documented earlier (Bhatkar and Kloft, 1977 ; Bhatkar, 1979a, b) ; those on Formicinae are summarized in Tables II and III and Fig. 2. In all the experiments, adults over 4 days of age were used. The donors usually contained 10-100 times more food (cpm) than they lost to the aggressive recipients. The background radioactivity (10-12cpm) was subtracted from all the readings and the means (rounded to nearest zero) of 10-12 replications are shown in the tables. Only those experiments where all the recipients had radioactivity within the first 1 h exposure are considered.

F. (Formica) polyctena worker received regurgitate from *F. pratensis, F. aquilonia, F. lugubris* and *F. rufa*, and *rufa* and *pratensis* offered almost twice the amount as *aquilonia* and *lugubris* (Table II). *C. ligniperda* gave more food to *F. polyctena* workers than *F. (Coptoformica) exsecta. F. (Raptiformica) sanguinea* received more regurgitate from *C. ligniperda* than the species

Table II – Interspecific worker-to-worker and queen-to-worker food exchange in Formicinae

Tabelle II – Interspezifischer Futteraustausch zwischen Arbeiterinnen und Königinnen-Arbeiterinnen bei Formicinae

Donor/caste	Recipient/caste	cpm transfer $\bar{X} \times 10^2$
Formica rufa ☿	*Formica polyctena* ☿	38.8
Formica pratensis ☿	*Formica polyctena* ☿	37.5
Formica lugubris ☿	*Formica polyctena* ☿	13.9
Formica aquilonia ☿	*Formica polyctena* ☿	15.5
Formica exsecta ☿	*Formica polyctena* ☿	1.9
Camponotus ligniperda ☿	*Formica polyctena* ☿	4.9
Camponotus ligniperda ☿	*Formica rufa* ☿ (monogynous)	1.5
Camponotus ligniperda ☿	*Formica lugubris* ☿	3.4
Camponotus ligniperda ☿	*Formica aquilonia* ☿	1.9
Camponotus ligniperda ☿	*Formica exsecta* ☿	3.0
Camponotus ligniperda ☿	*Formica sanguinea* ☿	7.4
Formica pratensis ♀	*Formica rufa* ☿	6.2
Formica pratensis ♀	*Formica polyctena* ☿	10.1
Formica pratensis ♀	*Formica lugubris* ☿	44.3
Formica pratensis ♀	*Formica aquilonia* ☿	61.7
Formica pratensis ♀	*Formica sanguinea* ☿	2.5
Formica pratensis ♀	*Formica rufibarbis* ☿	5.9
Formica lugubris ♀	*Formica rufa* ☿ (monogynous)	21.7
Formica lugubris ♀	(polygynous) ☿	20.9
Formica lugubris ♀	*Formica pratensis* ☿	83.1
Formica lugubris ♀	*Formica polyctena* ☿	18.5
Formica lugubris ♀	*Formica exsecta* ☿	19.7
Formica lugubris ♀	*Formica sanguinea* ☿	5.8
Formica lugubris ♀	*Camponotus ligniperda* ☿	26.4
Lasius niger ♀	*Formica polyctena* ☿	49.6
Lasius niger ♀	*Formica lugubris* ☿	6.1

of *F. rufa* complex, such as *F. polyctena, F. lugubris, F. aquilonia,* and *F. rufa*, in that order. *F. rufa* occurs in mutually exclusive monogynous and polygynous populations and *F. polyctena* populations are common to both. In *F. rufa*, the monogynous colony members gave less food to polygynous colonies but the reverse was not true. Also, more food was offered to *F. polyctena* workers by polygynous than by monogynous *F. rufa* colony members (Fig. 2). Even the queens (alates and apterous) of *F. pratensis* transferred regurgitate to the workers of *F. aquilonia, lugubris, polyctena* and *rufa*, in that order. *F. (Serviformica) rufibarbis* of *F. fusca* group received more amount than the enslaving species, *F. (Raptiformica) sanguinea* from the *F. pratensis* queens. *F. pratensis* workers were given more food by *F. lugubris* queens than *F. polyctena* or mono- or polygynous *F. rufa* workers. Also, *C. ligniperda* acquired more regurgitate from *F. lugubris* queens than did *F. polyctena, F. rufa* or *F. exsecta. L. niger* queens offered food to the workers of *F. lugubris* and *F. polyctena* but *L. niger* workers were never seen to do so and they never received food from any of the above species during

Table III – Interspecific male-to-worker and queen-to-queen food exchange in Formicinae

Tabelle III – Interspezifischer Futteraustausch zwischen Männchen-Arbeiterinnen und Königinnen bei Formicinae

Donor	Recipient	cpm transfer $\bar{X} \times 10^2$
Formica rufa ♂ (polygynous)	Formica polyctena ☿	3.5
Formica rufa ♂ (polygynous)	Formica pratensis ☿	12.1
Formica pratensis ♂	Formica polyctena ☿	1.2
Formica pratensis ♂	Formica rufa ☿ (monogynous)	0.6
Formica pratensis ♀	Formica polyctena ♀	7.7
Formica pratensis ♀	Formica nigricans ♀	16.4
Formica pratensis ♀	Formica fusca ♀	2.0
Formica pratensis ♀	Lasius niger ♀	19.7
Formica lugubris ♀	Lasius niger ♀	2.9

several repeated experiments. The males of *F. rufa* and *F. pratensis* were observed to offer regurgitate differentially to the workers of the alien species (Table III). The males of *F. rufa* (polygynous) offered more regurgitate to the workers of *F. pratensis* than to *F. polyctena* ; a small amount of food was received by the males and workers from *F. rufa* (polygynous) (not shown). *F. pratensis* males were less receptive donors to *F. rufa* workers (monogynous colonies) and receptive donors to *F. polyctena* workers or *F. rufa* (polygynous) males. The queens of Formicinae were selective in terms of food exchange (Table III). The queens of *F. nigricans* received more regurgitate from those of *F. pratensis* than did the queens of *F. polyctena*, and *F. fusca* seemed to receive the least amount. *L. niger* queens received more food from *F. pratensis* than from *F. lugubris.*

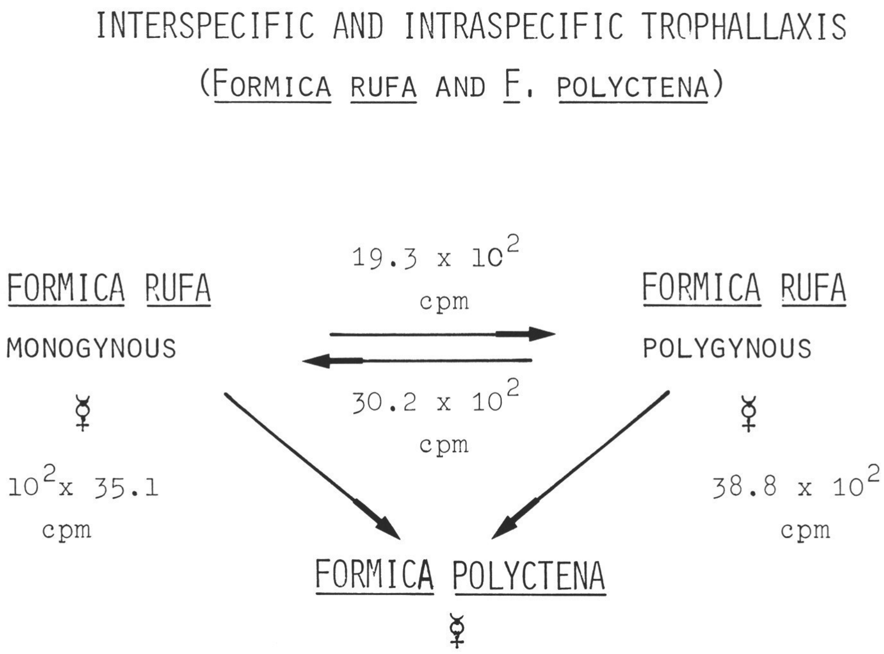

Fig. 2 – Inter- and intra-specific worker-to-worker trophallaxis in *Formica rufa* and *F. polyctena*

Abb. 2 – Inter- und intraspezifischer Futteraustausch zwischen Arbeiterinnen von *Formica rufa* und *F. polyctena*

Behavior during interspecific trophallaxis

The confronting individuals elicited various degrees of aggression specific to the species in question. The donors and aggressors antennated, contacted one another, regressed, opened mandibles and attacked. *Solenopsis* spp. raised the gasters, pointing them in the direction of the attacker and secreted droplets of venom. Mandibular attacks, holding fast on to the appandages and severing them was common to *Pheidole* spp. *F. exsecta* and *C. ligniperda* held the mandibles and cervices of the donors and severed their appandages under extreme aggression. Similarly, *F. sanguinea* was equally aggressive towards *L. niger* workers and queens. The initial aggression seemed to wane after 2-5 min when the donors exuded a droplet of regurgitate between the mandibles and oriented it in offering fashion to the aggressor/s. The formicines sprayed their donors with the formic acid via the acidopores. Self-grooming was a rule in all the satiated recipients. In exceptional cases, such as when *F. pratensis* queens offered food to *F. sanguinea* workers, the queens groomed the workers. The *Lasius* queens and *C. ligniperda* workers resumed ambulation, as if to show distress, and moved away from the attacker. This was also common to many Myrmicinae. The queens of *F. pratensis* with malformed wings were superior donors to those with normal wings when both were exposed to *F. polyctena* workers, and food transfer occurred much more readily (Fig. 1).

DISCUSSION

The exchange of alimentary liquids, either unilaterally or mutually, between the members of different species is termed interspecific trophallaxis (Bhatkar and Kloft, 1977) ; the intraspecific, intercolonial or intracolonial trophallaxis follow as a corollary (Bhatkar, 1979b). All these forms of food exchange occur in higher Myrmicinae and Formicinae and seem to be vital to the species associations and colony organization. Trophallaxis within the colony members may occur in the most ritualized fashion. The donors may need tactile stimuli through the antennal contacts at the base of scapes, mandibles or palpi or through the grooming of abdomen, legs, thorax, cephalic ventrum, reaching progresssively to the labium. A droplet of regurgitate finally oozes between the mandibles of the donor and is available to the solicitor. Wallis (1961) brought out the role of foreleg stroking in addition to vigorous antennation during trophallaxis. Persistent solicitation (as it appears to be) by the same individual may lead to distress antennation in the donor and eventual turning away from the solicitor (Bhatkar, 1979a, b). There may be a series of such codes by which ants demand, accept or reject trophallactic fluid (Lenoir and Jaisson, 1974).

Under the aggressive stress from an alien, the donor's behavior becomes ritualized. It antennates the alien, regresses, moves away from the site of attack and if attacks or aggressive solicitation persist, regurgitates a droplet of fluid between its mandibles. The droplet is oriented to the attacker's head with vibrant antennation. The overall responses are quick, intense and any delay in food offering may result in an overt form of aggression in the alien recipient. It may involve mandibular attacks, seizing, pulling, grappling or severing appandages, petiole or cervix and may associate with stinging (in Myrmicinae) or spraying (in Formicinae). The donor moves towards the solicitor/aggressor and antennates it, as if invoking a solicitation response and supressing aggression. The element of aggression in the solicitor seems to be decisive as to whether trophallaxis will occur or not. For example, *F. Pratensis* queens with malformed wings were much more susceptible to the aggression from *F. polyctena* workers and offered food quicker than the alate queens that showed initial aggression by opening mandibles towards the attacker (fig. 1). Among the symbiotic species, such as temporary parasites (*F. rufa, F. pratensis, F. lugubris, F. aquilonia, F. exsecta*) and their hosts (*F. fusca, F. rufibarbis, F. polyctena*, etc.) (Gösswald, 1951 ; Kutter, 1964, 1969), or dulotic species (*F. sanguinea, Polyergus rufescens*) (Beck, 1961) and their hosts (*F. fusca, F. rufibarbis, F. pratensis, F. rufa, F. polyctena*) (Bernard, 1968), antennation, mandibular widening, seizing and pulling seem to result in regurgutative offering by the hosts. In the species where no symbiosis is established, such as *S. invicta, S. geminata, P. dentata, P. morrisi, C. ligniperda* (tribe Camponotini), *L. niger* (Formicini), more intense attacks by the aggressors incited interspecific trophallaxis.

There seems to be a differential aggressivness among different castes of workers engaged in food exchange. The minors and majors of *S. geminata* are more receptive to similar castes in *S. invicta* than the majors of *S. geminata* to the minors of *S. invicta*. The majors and minors of *P. dentata* offered more food to the dissimilar castes of *S. invicta* (Bhatkar and Kloft, 1977). More the aggressive encounters, better is the receptiveness of the donor. When otherwise aggressive minors of *S. invicta* were exposed to 4 times their number of *S. geminata* minors or *P. dentata* majors, *S. invicta* offered regurgitate to the latter species. The confrontations between polymorphic workers of *S. invicta* and majors and minors of *S. geminata* or *P. dentata* indicated that *S. invicta* workers are 3 times as aggressive as *P. dentata* majors, 3 times as aggressive as majors and minors together and twice as aggressive as *S. geminata* workers (Bhatkar, 1973).

Interspecific food exchange occurred in response to the aggression by a potential recipient against a satiated individual. But not all the species, such as those nesting in the annually burned vegetational habitats in North Florida, show such a behavior. *P. dentata* and *S. geminata* are regarded as the ecological competitors of *S. invicta* (Wilson, 1976 ; Bhatkar and Whitcomb, 1981). *S. geminata, P. dentata* and *P. morrisi* invariably offered food to more aggressive *S. invicta*. Further, laboratory colony invasion studies indicated that satiated donors of these species were able to delay the invasion of the first batch of *S. invicta* entrants by 20-30 min and more workers were recruited to the entrance while the queen and the brood were moved away to a safer place by the nurses underground. The majors of *Solenopsis* and *Pheidole* are replectic (store liquid for a long duration), thus better suited for such an obscure form of defense. The degree of aggressiveness in the contestants which may itself be age dependent (Fielde, 1903 ; Bhatkar, unpublished), satiation of the donors and overall intrinsic potential of the species to exchange food seem to decide the occurrence of interspecific trophallaxis between them.

Thus far, interspecific trophallaxis in Myrmicinae and Formicinae was limited to the subfamilies and occurred beyond specific, subgeneric, generic and tribal levels. The evolutionary and adaptive significance of this phenomenon may lay in a rather subtle explanation of the intrinsic potential of the species for «allotrophallaxis». Several closely related forms of *Formica* and *Lasius* occur in palearctic and nearctic regions (Creighton, 1950 ; Betrem, 1960 ; Kutter, 1965 ; Buren, 1968). In *F. rufa* group itself, species are difficult to separate even on the basis of their genitalia (Betrem, 1960). For such instances, if one considers that the parent population fragmented and diverged genetically through geographical and ecological barriers, then the reinvading species thus formed may enter into certain host-parasite relationships. This Emery's rule (Wilson, 1971) can be projected to its further repercussion. First, the genetic divergence of the species in *F. rufa* group prevents them from interbreeding (Betrem, 1960) and disjunct populations of *F. polyctena, F. lugubris*, etc. exist (Gösswald et al., 1965). A similar situation seems to be true to *S. saevissima* complex in the Brazilian flood plain region (Buren et al., 1978) wherefrom *S. invicta* and *S. richteri* found their entry to the southeastern U.S. during 1930s and 1920s respectively. *S. geminata* complex of the Mexican humid tropics poses a parallel problem (Bhatkar, unpublished) and of this red and black forms occur in the southern U.S. *Pheidole* is an expanding genus from Miocene times and *Camponotus* from Oligocene times (Brown, 1973). Under such situations, various forms of parasitisms must occur as a rule. Secondly, one of the intrinsic isolating mechanisms in the speciating forms may be the conceivably less understood colony or species odors that seem to cause aggression in ants. Such an aggression seems to be subdued in the presence of the regurgitate from the ant to be aggressed upon during intercolonial or interspecific confrontations (Bhatkar, 1979a). The associated behavior of the donor appears to be analogous to appeasement in the higher animals (Bhatkar and Kloft, 1977).

F. polyctena, F. lugubris, F. aquilonia, F. pratensis and *F. truncorum* are polygynous and polydomous (Betrem, 1960). Under the competitive pressure from *F. polyctena* and *L. fuliginosus, F. rufa* apparently resorts to polygyny (Kutter, 1964) and the same seems to be true in *S. geminata* and *S. invicta* (Bhatkar, 1979b). Social parasitism is realized through facultative polygyny (Buschinger, 1970), and an intermediate state of temporary parasitism is achieved through colony founding by the mated queens in the colonies of specialized nursing hosts. Interspecific trophallaxis should find its adaptive value especially when several oligogynous or polygynous species occur in the same geographical area, find entry in new regions of their establishment or exploit the same habitat. In the present investigation, *F. polyctena* received more regurgitate from *F. rufa, F. pratensis, C. ligniperda* inhabiting boreal habitats than from *F. lugubris, F. aquilonia* or *F. exsecta* inhabiting boreo-Alpine habitats. The queens and males of temporary parasites or dulotic species seem to be selective in their food offering response. The queens of *F. pratensis, F. rufa, F. lugubris*, and *F. polyctena* are known to found their colonies in those of the species of *F. fusca* group (Gösswald, 1951 ; Kutter, 1964), and can be conjectured to offer less food to their hosts than they would receive. *F. sanguinea* is known to occasionally parasitize *F. pratensis* colonies (Bernard, 1968).Thus, *F. pratensis* queens, usually killed by *F. sanguinea*, offer little food to the hostile *F. sanguinea*. Interspecific trophallaxis seems also to be concurrent with the presence of polygyny. Both workers and males of the polygynous *F. rufa* colonies were more receptive to the workers of *F. polyctena, F. pratensis* and *F. rufa* (monogynous) than those of monogynous *F. rufa* colonies. Food exchange is known to occur between the members of *F. polyctena* and *F. rufa* in nature (Chauvin et al. 1961, Gösswald and Kloft, 1963). The founding queens of some species like *L. niger* develop a thoracic dilation of their alimentary tract (Mura, 1973) that seems to facilitate their food offering trait, as against their workers, when confronted with the aggressive queens of *F. pratensis* or workers of *F. polyctena* and *F. lugubris*. It seems that since *F. polyctena* nests in the habitats of mono- and polygynous *rufa*, it obtains regurgitate from both of these forms. The nesting of *F. rufa, F. truncorum, F. polyctena, F. exsecta* and *L. fuliginosus* in proximity prompted Kutter (1964) to conduct his alliance colony experiments. The occurrence of interspecific trophallaxis between the species with no apparent symbiotic relationship, such as *S. invicta, S. geminata,* *P. dentata, P. morrisi* in Florida or *C. ligniperda, L. niger, L. flavus* and *L. fuliginosus* in Central Europe may be a relict trait that was carried over as adaptive, to facilitate the close nesting among aggressive species in their shared habitats. In the light of the present discussion, food exchange between the species of different subfamilies, such as *Formicoxenus nitidulus* cohabiting the nests of *F. pratensis* and *F. rufa* (Wheeler, 1910 ; Stumper, 1950), or between *Crematogaster limata parabiotica* associated parabiotically with *Camponotus femoratus* and *Monacis debilis* (Wheeler, 1921 ; Swain, 1980), or that between *C. floridanus* and *S. invicta* (Wilkinson et al., 1978), may involve a complex semiochemic convergence relative to their behavior and needs a further study.

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QUELQUES DONNÉES SUR LA BIOLOGIE DES FOURMIS LIOMETOPUM (DOLICHODERINAE) DU MEXIQUE ET EN PARTICULIER SUR LEURS RAPPORTS AVEC LES HOMOPTERES

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RÉSUMÉ

Dans le cadre d'une étude générale de la biologie et de l'écologie des fourmis *Liometopum* du Mexique, on a recensé 2 espèces alors que, jusqu'ici, on n'en connaissait qu'une dans ce pays. Elles vivent dans des biotopes généralement différents, mais pour les deux, la source alimentaire de prédilection est constituée par des coccides, dont on a recensé les espèces en fonction de leur importance dans l'alimentation de ces fourmis.

SUMMARY

Some records about the biology of the ants Liometopum **(dolichoderinae) of Mexico and their relationships with some Homoptera**

Because one new species of *Liometopum* has been recently discovered, we know that 2 species of this ant are living in Mexico. Although their biotopes are generally different, both feed on Coccidae, the species and importance of which have been enumerated.

Fig. 1 – Distribution potentielle des Escamoles au Mexique (en grisé)

Fig. 1 – Potential distribution of the «Escamoles» in Mexico (in grey)

INTRODUCTION

Les fourmis du genre *Liometopum*, bien que largement répandues en Amérique du Nord, ont peu retenu l'attention des chercheurs. Cela est dû, sans doute, en partie, à la difficulté de localiser les nids. Nous nous sommes intéressés à ces fourmis, car au Mexique, les stades immatures des sexués sont récoltés annuellement et consommés sous le nom d'«escamoles». Ces insectes représentent un apport protéique non négligeable pour les populations qui les exploitent, et différentes analyses ont montré qu'il s'agissait véritablement d'une source alimentaire de qualité (Conconi et Bourges, 1977 ; Conconi et Pino, 1980).

Pour le Mexique, on ne connaissait jusqu'ici que l'espèce *L. apiculatum* (Mayr) ; or, nos prospections ont montré qu'il existe aussi *L. occidentale luctuosum* Wheeler. Cette espèce avait été précédemment répertoriée aux Etats-Unis dans les états de l'Utah, de l'Arizona et surtout du Colorado (Gregg, 1963). Ces deux espèces, indifféremment exploitées au Mexique, constituent des nids hypogés dont les constructions sont très particulières : ils sont formés de trabécules de terre agglomérée, anastomosés en réseau. Le couvain est élevé dans les mailles de ce réseau.

DISTRIBUTION GÉOGRAPHIQUE DES DEUX ESPÈCES, ÉCOLOGIE

Au Mexique les fourmis *Liometopum* se rencontrent entre les 19ème et 21ème parallèles de latitude Nord et les 97,7ème - 101ème de longitude Ouest, occupant des zones arides et semi-arides (*L. apiculatum*) jusqu'à des zones forestières (*L. occidentale*). Elles s'établissent généralement dans des sols en pente et très souvent au niveau d'un lacis de racines de divers végétaux pérennes tels que *Agave sp.*, *Opuntia sp.*, *Myrtillocactus geometrizans, Yucca filifera, Senecio praecox, Schinus molle* ou *Prosopis juliflora* pour *L. apiculatum*, ou *Quercus sp.*, *Juniperus sp.* et *Pinus sp.* pour *L. occidentale luctosum*. Ces deux espèces s'opposent donc à l'espèce européenne *L. microcephalum* qui établit son nid dans les arbres.

L. apiculatum se rencontre donc le plus souvent dans des biotopes à buissons xérophytes (Matorral xérofito de Rzedwski, 1978) avec un climat allant du type B_{S_1} KW (c'est-à-dire le plus sec de la gamme des climats dits secs, avec un coefficient $P/T > 22,9$) à un climat de type C (wo) (c'est-à-dire le plus sec des climats tempérés subhumides, avec un coefficient $P/T < 43,2$). *L. occidentale luctosum* se trouve dans les zones de conifères et de chênes (Rzedwski, 1978), où les climats vont du type C (Wo) comme précédemment,

Tableau I – Préférence alimentaire de *Liometopum* pour différentes espèces de Coccides en plusieurs localités

Table I – Food preference of *Liometopum* to different species of Coccids in various localities

		Liometopum apiculatum										*L. occidentale luctuosum*	
	Espèces	Etat de Hidalgo								District Fédéral		Etat de Michoacan	
		Cardonal		Tulancalco		Tulancingo		Santuario		Tlaltenco		Tlalpujahua	
		A	B	A	B	A	B	A	B	A	B	A	B
	Neolecanium herrera	++++	+++										
O	*Coccus pseudomagnoliarium*		++++										
O	*Ovaticoccus agavium*		++++										
	Puto yuccae	+	+	+++ *Agave* ++ *Myrtillocactus*	+++ *Agave* ++ *Myrtillocactus*								
	Eurycoccus copallinae	++++	+++										
	Anicococcus sp. 1	+	+										
O	*Anicococcus* sp. 2		++++										
	Saissetia olleae			++++	+++								
	Acutaspis agavis			+	+								
O	*Odonaspis* sp.				++++								
O	*Eriococcus* sp.				++++								
O	*Orthezia* sp.				++++								
	Pseudococcus agavis					++++				++++	++++	++++	
	Ceroplastes sinensis							++++	+++				
O	*Cataneococcus olivaceus*								+++				
	Saissetia nigra									++++	++++		
	Klemiberlesia cetanie									+	+		
O	*Anisococcus* sp. 3										++++		
	Crissicoccus sp.											+	

A : en l'absence de plantes annuelles
B : en présence de plantes annuelles
O : Coccides rencontrés uniquement sur des plantes annuelles

A : without annual plantes
B : with annual plants
O : Coccids only on annual plants

au type C (Wa) qui est le climat le plus humide des tempérés subhumides (coefficient $P/T > 55{,}0$).

Il semble qu'un des facteurs limitant l'extension de la très vaste distribution de ces fourmis (figure 1) soit l'altitude : dans les régions que nous avons prospectées on ne les rencontre qu'entre 2000 et 3000 mètres. Bien que les conditions écologiques semblent favorables nous n'avons pu en rencontrer au-dessous de 1800 mètres. Il semblerait qu'il y ait une corrélation entre altitude et latitude car plus on remonte vers le nord et plus les exigences altitudinales diminuent, selon les indications de collecte de ces fourmis aux Etats-Unis (1316 à 2438 mètres pour *L. apiculatum* et 1219 à 2438 mètres pour *L. occidentale luctuosum*).

ALIMENTATION DE CES FOURMIS

Comme la plupart des fourmis, les *Liometopum* étudiées sont omnivores. Nous les avons vues se nourrir aussi bien de reliefs alimentaires divers (viande, œufs, fruits, pain) que de sécrétions de plantes ou d'insectes (aphides, membracides, coccides). Pour joindre une source alimentaire, elles établissent des chemins atteignant, parfois, plus de 100 mètres de long.

Chez *L. occidentale luctuosum*, les galeries de cheminement courent sous la couche de feuilles jonchant le sol. Cette protection pourrait expliquer pourquoi les fourmis s'y rencontrent à toute heure du jour. Au contraire, *L. apiculatum* balise ses chemins presque uniquement en surface ; et lorsque la température s'élève fortement au milieu du jour, les fourmis interrompent leur circulation et restent abritées sous les pierres.

RELATIONS AVEC LES COCHENILLES

Bien que ces fourmis soient omnivores, nous avons remarqué que les exsudats d'homoptères constituent l'essentiel de leur alimentation. Et ce sont les cochenilles qui semblent assurer la majeure partie des récoltes.

Le tableau I montre les différentes espèces de cochenilles visitées par les fourmis. Nous voyons que, lorsque les plantes annuelles sont bien développées, les fourmis auront tendance à les fréquenter davantage pour prospecter leurs cochenilles, délaissant à cette occasion les hôtes des plantes pérennes.

Notons enfin que dans la zone forestière de Tlalpujahua (Michoacan), la cochenille *Crassicoccus sp.* vit sur le chêne, où elle est abondante. Toutefois, elle est fort peu visitée par les fourmis (*L. occidentale luctuosum*) qui lui préfèrent *Pseudococcus agavis* (sur agave).

RELATIONS AVEC LES MEMBRACIDES

Nous avons récolté l'espèce *Vandurea segmentata* sur *Myrtillocactus geometrizans*. Ce membracide a déjà été signalé pour être en relation avec *Liometopum* au Texas (montagne de Chisos) par Van Pelt, 1971) mais la plante hôte était différente.

RELATIONS AVEC LES APHIDES

Nous avons trouvé trois espèces du genre *Aphis*, deux en relation avec *L. apiculatum* et une avec *L. occidentale luctuosum*.

En conclusion, nous pouvons dire que la biologie de ces fourmis est loin d'être monotone et mérite d'être mieux connue.

REMERCIEMENTS. – Nous remercions le Docteur Bernadette Darchen (Station Biologique de l'Université Pierre et Marie Curie, Les Eyzies, France) pour son aide dans l'exécution de cette recherche et le Docteur R. Gregg pour l'identification des espèces.

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THE FUNGUS GROWING ANTS

HOST PLANT SELECTION BY AN ATTINE ANT

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SUMMARY

Although leafcutting (*Atta*) are highly polyphagous insects, many plant species readily available to the ants in nature escape ant attack nearly completely. It is reasonable to suppose that at least some of these plant species are avoided because they are chemically defended against the ants, containing substances toxic to the ants, to their food fungus, or to both. We have been studying the host plant preferences of *Atta cephalotes* in the laboratory and in nature in Santa Rosa National Park, Costa Rica. We report here on the development and use of a rapid bioassay for testing ant preferences for leaves in the field. Our results show that the ants collectively exhibit a continuously graded response when presented with a simultaneous choice of leaves from a large number of species. The results also indicate that the ants are capable of making very subtle distinctions in leaf quality, not only between species, but also between individual plants within species, and even between leaves from different parts of the same plant. We also describe a laboratory bioassay for testing the repellency of chemical extracts of plant species most often avoided by the ants. Using this laboratory bioassay, we have isolated specific ant repellents from several plant species from Santa Rosa. The first of these repellents to be completely characterized, caryophyllene exposide, has proven to be a potent fungicide, lethal in small doses to the ant's fungus.

RESUMEN

Selección de la planta huésped por una hormiga Attine

Aunque las hormigas cortadoras de hojas (*Atta*) son insectos polífagos, muchas especies de plantas facilmente disponible para ellas en el campo escapan a su ataque. Es razonable presumir que al menos unas de estas especies pueden ser evitadas por las hormigas en razón de tener algún tipo de protección química que puede ser tóxica tanto para las hormigas, como para el hongo que ellas cultivan, o para los dos.

Hemos estudiado las preferencia de *Atta cephalotes* en cuanto a la planta huésped en el laboratorio (nido en catividad) y en el campo (Parque Nacional de Santa Rosa, Costa Rica). Se relata aquí el desarrollo y uso de un rápido bioensayo para probar las preferencias de las hormigas en el campo. Los resultados indican que las hormigas tienen colectivamente una repuesta continuamente graduada cuando son presentadas con una selección simultánea de hojas de muchas especies. Los resultados del bioensayo también muestran que las hormigas tienen la capacidad de hacer distinciones muy sútiles en la calidad de las hojas, no sólo entre especies, sino también entre plantas individuales a dentro de las especies y también aún entre hojas de diferentes partes de la misma planta. Se describe además un bioensayo en el laboratorio para probar la repelencia de extractor químicos de especies de plantas normalmente evitadas. Usando este bioensayo en el laboratorio, hemos aislado, de algunas especies de plantas de Santa Rosa, repelentes específicos contra las hormigas. El primero de estos repelentes caracterizado, el epóxido de cariofilene, es un fungicida potente, letal en dosis muy pequeñas, para el hongo de las hormigas.

INTRODUCTION

Leafcutting ants of the genus *Atta* (Hymenoptera, Formicidae, Attini) are highly polyphagous herbivores, attacking a large number of plant species in a diverse array of plant families. Adult ants feed primarily on plant sap, taken while they cut and mulch leaves (Littledyke and Cherrett, 1976 ; Quinlan and Cherrett, 1979), and supplement their diet with fungus. Larvae feed exclusively on hyphal juice from a specific fungus, *Rhozites gongylophora*, cultivated in underground gardens on the collected leaves (Weber, 1972).

The ant-fungus mutualism has made attines among the most successful and abundant insect herbivores in the neotropics, elevating them to pest status in many areas. The fungus makes available a broader selection of potential host plant species by transforming plant material that would otherwise be indigestible, toxic, or simply unpalatable (Boyd and Martin, 1975a, b). A number of fungal digestive enzymes pass unaffected through the ant gut and are defecated onto the fungus garden, thereby hastening the penetration of fungal hyphae into the leaf tissue. The enzymes function in the ant gut as well ; and Martin (1979) has recently suggested that attines and many other fungus-eating insects are primarily mycophagous to acquire digestive enzymes which the insects are unable to make themselves.

The fungus may also be a superior diet than plant sap for the larvae, which require better nutrition for growth than is required for maintenance of adult ants. Fungi have the capacity to concentrate biologically important elements such as nitrogen and phosphorus from extremely dilute sources (cf. Martin, 1979) ; and leaves and other plant tissues are frequently lower in nitrogen content than fungi (Mattson, 1980). Whether *Rhozites* has higher available protein N than the bulk of the leaf material collected by *Atta* is not presently known, however.

Although the ants are highly polyphagous, it has been known for some time that the ants rarely or never cut many plant species they encounter in nature (e.g., Cherrett, 1968 ; Rockwood, 1975, 1976). A number of factors have been suggested as important in the decision by leafcutting ants to cut or reject a particular set of leaves. These include : (1) secondary compounds which are toxic to the ants, their fungus, or both ; (2) secondary compounds which possibly reduce the digestibility of the plant material by the ant or its fungus, such as tannins (Feeny, 1970) ; (3) the nutritional value, including usable protein, carbohydrate, and lipid constituents, as well as trace essential substances such as steroids (Waller, pers. comm.) ; (4) mechanical defenses of the plant, including leaf toughness, trichome density, and gluey or copious sap, especially latex saps (Stradling, 1978) ; and (5) the moisture content of leaves (Janzen, Bowers, pers. comm.). In addition, a particular colony of ants may not cut an otherwise acceptible plant species because of : (1) the availability of superior host plant species (Hubbell and Rockwood, 1983) ; (2)history effects such as where trail systems develop and ant experience with some plant species and not others ; (3) retrieval costs which are too great (e.g., plants are too distant) ; (4) competition from rival colonies in adjacent territories ; and (5) the presence of aggressive ant species (Cherrett, this volume).

We have been studying the natural foraging patterns of *Atta cephalotes* in semi-decidous forest in Santa Rosa National Park, Costa Rica (Hubbell and Rockwood, 1983 ; Hubbell, Stevens, and Wilson, unpubl.). A year-long study of foraging by 20 colonies revealed strong seasonality in cutting patterns, confirming the findings of Rockwood (1975, 1976). Two pronounced patterns attracted our attention. First, colonies exhibited graded cutting responses, such that the amount of leaf material harvested was lognormally distributed over plant species ; and it could be shown that the lognormal was not derived from plant abundances. Hubbell and Rockwood (1983) proposed that the ants have built-in graded responses to leaves based on their relative suitability as substrate for growth of their fungus.

The second pronounced pattern was the tendency for the ants to attack plants flushing new leaves, a pattern seen in both evergreen as well as deciduous species. Preference for new leaves in leafcutting ants has been reported several times (e.g., Cherrett, 1972a ; Rockwood, 1975 ; Littledyke and Cherrett, 1978), but there has been little work on the causes of this preference. Cherrett (1972b) has suggested that old leaves might accumulate ant repellent substances ; subsequently, Littledyke and Cherrett (1978) showed that lipid extracts of old leaves were more repellent than extracts of young leaves in two tropical and four temperate species.

We have begun studying why the mature leaves of many plant species at Santa Rosa are completely or nearly completely avoided by *Atta cephalotes*. Initially, we have limited our efforts to determining more precisely which species and individual plants are repellent to the ants, and when they are repellent seasonally ; and to isolating and identifying chemically extractable ant repellents if they are present, using a laboratory bioassay to guide the isolation procedure. In this paper we report on the development of a rapid bioassay of leaf preferences for use in the field, and on some results of its application in studying seasonal changes in leaf preferences in Santa Rosa *A. cephalotes* colonies. We then describe the laboratory bioassay and our initial progress in characterizing ant repellents from several species avoided by the ants.

We organize our discussion around a consideration of the following hypotheses : (1) Leafcutter ants will exhibit continuously graded leaf preferences when a large number of species is presented to them at one time for choice ; (2) Colonies will show marked seasonal changes in leaf preferences among the same set of plant species ; (3) Within plant species, the ants will prefer leaves of some individuals over others ; (4) Within individual plants, the ants will prefer some leaves over others, especially new leaves over old, and sun leaves over shade leaves ; (5) Ants will prefer species with high nitrogen content over species with low nitrogen content ; (6) Mature leaves of at least some of the avoided species are not cut by the ants because they contain chemicals repellent and/or toxic to the ants or their fungus ; and (7) Both polar (e.g., phenolics) and nonpolar (e.g., terpenoids) compounds will be isolated as potent ant repellents.

PROCEDURE

Field leaf preference tests

Leaf preference tests were carried out in Santa Rosa National Park, Guanacaste Province, Costa Rica, on colonies of *Atta cephalotes* studied previously (Hubbell and Rockwood, 1981 ; Hubbell, Stevens, and Wilson, unpublished). Tests were made on colony 5, 16 in July, 1980, and on colonies 5, 16, 6, 20, and 7, 22 in October, 1980, months which represent early-middle and late wet season, respectively. In the main set of preference tests, the ants were given a simultaneous choice of 20 species in 18 plants families (Table I), selected at random from 150 tree and shrub species known to occur in the forest. All 20 species were represented by leaves taken from a single, known individual, and the same tree or shrub in both July and October as well. An attempt was made to pick only mature, sunlit leaves for the choice tests.

Table I – Primary group of 20 species, and family ; secondary group of species, and family

Tabla I – Grupo primario de especies, y familia ; grupo secundario de especies, y familia

Primary set of 20 species	Family	Second set of species	Family
Allophylus occidentalis	Sapindaceae	*Acacia collinsii*	Mimosaceae
Annona purpurea	Annonaceae	*Alibertia edulis*	Rubiaceae
Bombacopsis quinata *	Bombacaceae	*Astronium graviolens*	Anacardiaceae
Bursera simaruba	Burseraceae	*Bombacopsis quinata* *	Bombacaceae
Calycophyllum candidissimun	Rubiaceae	*Casearia sylvestris*	Flacourtiaceae
Chlorophora tinctoria	Moraceae	*Cedrela odorata*	Meliaceae
Chomelia spinosa	Rubiaceae	*Cordia alliodora* *	Boraginaceae
Cordia alliodora *	Boraginaceae	*Euphorbia schlectendahlii*	Euphorbiaceae
Exostema mexicanum	Rubiaceae	*Ficus* sp.	Moraceae
Hemiangium excelsum	Celastraceae	*Genipa americana*	Rubiaceae
Hymenaea courbaril *	Papillionaceae	*Hymenaea courbaril* *	Papillionaceae
Licania arborea	Chrysobalanaceae	*Luehea speciosa* *	Tiliaceae
Luehea speciosa *	Tiliaceae	*Muntingia calabura*	Elaeocarpaceae
Malvaviscus arboreus	Malvaceae	*Quercus oleiodes*	Fagaceae
Manilkara zapota	Sapotaceae	*Randia lasianthea*	Rubiaceae
Ocotea veraguensis	Lauraceae	*Sapium thelocarpum*	Euphorbiaceae
Piper amalgo	Piperaceae	*Spondias mombin*	Anacardiaceae
Simarouba glauca	Simaroubaceae	*Tabebuia chrysantha*	Bignoniaceae
Spondias purpurea	Anacardiaceae	*Trichilia colimana*	Meliaceae
Trichilia cuneata	Meliaceae	*Verbesina gigantea*	Compositae
		Zanthoxylum setulosum	Rutaceae

* Species in common between the two lists

Uniform 38 m^2 leaf disks were punched from the leaves of each species. All species were offered simultaneously to the ants, one disk per species, along active foraging trails to the colony, and in a way that all disks would be encountered frequently. As soon as any disk was picked up and carried into the nest, it was recorded and replaced by a new disk of the same species. At the end of 1 to 2 hours, the number of disks of each species taken by the ants was tallied. To eliminate possible position effects, the locations of species in the line of disks was randomized every 15 minutes in the July tests ; but this practice was discontinued after no position effects could be detected. It was necessary to do these tests on trails with a relatively controlled trail activity level. In initial experiments, we discovered an inverse relationship between number of species of leaf disks picked up and the number of laden ants returning to the nest with leaf fragments (Fig. 1). It appears that workers on very active trails are already committed to particular leaf resources and are less likely to pick up the leaf disks of less preferred species. We were able to control trail activity in our choice experiments to between 150 and 250 laden ants per half hour.

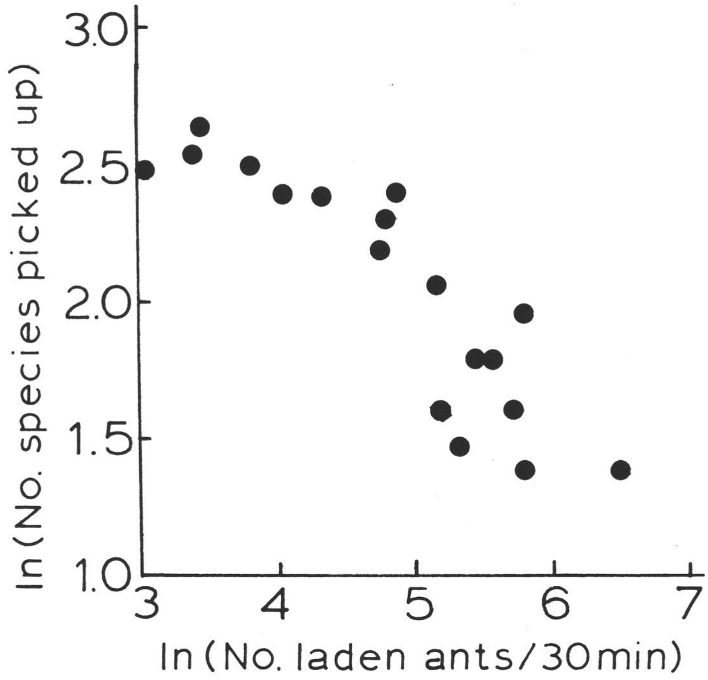

Fig. 1 – Inverse relationship between the number of species of leaf disks picked up by the ants in a given preference test, and the number of laden ants returning to the nest already carrying a leaf fragment. The axes are log transformed to reduce the graph scale.

Fig. 1 – Relación inversa entre el número de tipos de discos de hojas tomado por las hormigas en una prueba de preferencias, y el número de hormigas que regresan al nido trayendo un pedazo de hoja. Los ejes son transformados logaritmicamente para reducir la escala de la gráfica.

In October an additional 17 species were tested in combination with 4 species from the original list of 20 for standardization (Table I). We also tested for intraspecific and intra-plant variability in leaf palatability in 3 species in October. Comparisons were made between young versus old, and sun versus shade leaves in all combinations.

Laboratory biossay

Leaf extracts were tested for repellency in choice tests conducted on a laboratory *Atta cephalotes* colony. The colony consists of several hundred thousand workers and about 20 liters of fungus, and is maintained on a daily diet of 80 g of frozen lilac leaves. Choice tests were carried out on a foraging platform connected to the colony by a 2.5 cm diameter tube (Fig.1). The platform is a thin, hollow box of plexiglass. Ants arriving from the colony are released into the center of the box and from there disperse in all directions. Ants gain access to the test arena on the top surface via a ring of holes around the perimeter of the platform. The number of ants in the test arena and the direction of ant arrival can conveniently be regulated by opening or closing selected holes with rubber stoppers.

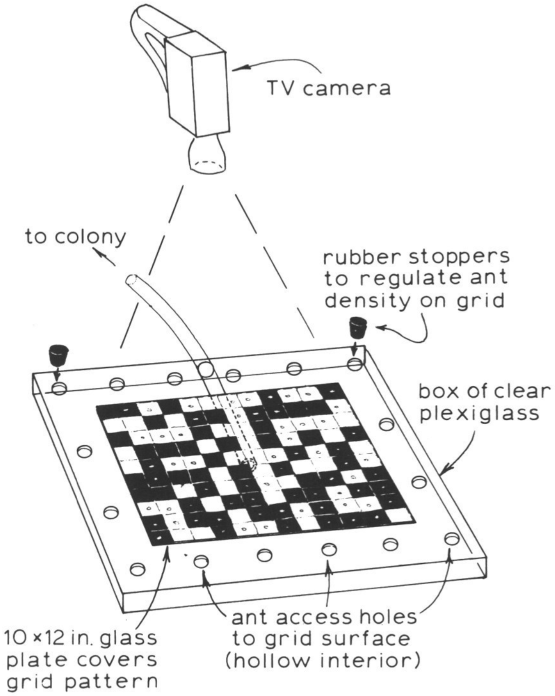

Fig. 2 – Hollow plexiglass foraging platform on which laboratory bioassays of leaf extracts are tested for repellency. The checkerboard pattern represents the computer-generated random grid design for locatinf control and test flakes.

Fig. 2 – Caja de plástico ahuecada usada como plataforma sobre la cual se realizaron los bioensayos en laboratorio para probar la repelencia de los extractos de hojas. El diseño en ajedrez representa el dibujo generado al azar para localizar las hojuelas control y de prueba.

Ants forage for pressed rye flakes, which serve as the carrier material for leaf extracts ; and the removal of flakes by the ants is videotaped (Fig. 2). Flakes are soaked in solvent (CH_2Cl_2) alone («control flakes») or in solvent plus leaf extract («test flakes») for 1 minute and air dried. Sixty control and 60 test flakes are then arranged according to a computer-generated random design in a 10x12 grid pattern. The printed design, which is legible on the TV monitor, is placed directly on the foraging platform and covered by a glass plate onto which the flakes are placed. A fresh plate, cleaned with acetone to prevent possible carryover of pheromone trails between trials, is used for each test. Once the flakes are in place, the ants are allowed onto the top of the platform (while setting up, all access holes are closed). During a run, the time is announced every minute and recorded on the audio channel of the videotape. On playback, the tape is stopped every minute for stop-action analysis of the number of remaining test and control flakes.

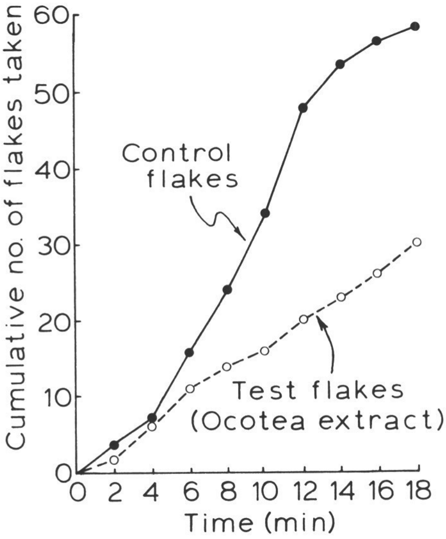

Fig. 3 – Typical bioassay test run results, in this case for the crude chloroform extract of *Ocotea veraguensis* leaves. There are 60 control and 60 test flakes containing the *Ocotea* extract. The difference is statistically significant at $p < 0.001$.

Fig. 3 – Resultados típicos de un bioensayo, en este caso para el extracto crudo en cloroformo de hojas de *Ocotea veraguensis* (60 huejelas control y 60 de prueba). La diferencia es estadisticamente significativa para $p < 0.001$.

Figure 3 shows the result of a typical bioassay, in this case of the crude chloroform extract of nature *Ocotea veraguensis* leaves. In this illustrative run, we continued the analysis until all of the control flakes had been removed (18 minutes). However, in general we need only analyze the tapes to the point at which half of the control or test flakes have been removed, whichever comes first. We then test the significance of the difference in number of control and test flakes removed using a modified binomial test. Thus, if 30 control flakes have been removed (half), and if the null hypothesis is that test flakes are no more repellent than control flakes, then we can reject the null hypothesis if the number of test flakes is : less than 23 ($p < 0.05$), less than 10 ($p < 0.01$), or less than 17 ($p < 0.001$), for a one-tailed test. Thus, the *Ocotea* chloroform extract is significantly more repellent than the control at $p < 0.001$. We have found that this method of bioassay gives very reliable and repeatable results. It is also very rapid, making feasible the analisys of large numbers of samples, such as are easily generated by column chromatography of a chemically complex leaf extract.

General chemical procedures

Although the late stages of isolation and characterization of ant repellents differ depending on the nature, novelty, and chemical complexity of the substances involved, the initial stages of extraction and partial separation do not change markedly. Using large capacity Soxhlet extractors, we extracted 100 g samples of leaves in chloroform to obtain the lipid-soluble, nonpolar substances, and in ethanol to obtain the polar substances. The solvent are evaporated, and the extracted material is weighed and then redissolved in a much smaller volume of solvent (usually methylene chloride). Samples of the redissolved extract are then bioassayed for repellency. Typically, one but not both fractions is active (more often the chloroform fraction). The remaining sample is washed with 1.0 HC1 to remove alkaloids, and 1.0 N NaOH to remove acids. These acid-soluble, neutral, and base-soluble fractions are then bioassayed. One or more of these fractions may be active. Each active fraction is further fractionated by column chromatography using gradient elution procedures. A series of 20 or more fractions is then obtained. These can often be reduced to a smaller set of samples by combining fractions judjed similar on the basis of thin layer and gas chromatographic analysis. Each of these fractions is then bioassayed individually for repellency. At this stage of separation, the activity is usually localized in one or at most a few samples, each of which contains a small number of compounds. The fractionation-bioassay cycle is repeated until pure compounds are isolated.

Thereafter we attempt to determine the structure of the ant repellent compounds using standard physical and chemical methods, including combined gas chromatography-mass spectrometry (GC-MS), proton and carbon nuclear magnetic resonance spectroscopy (NMR), and infrared (IR) and ultraviolet (UV) spectroscopy as needed. If spectral data do not provide sufficient information to characterize a compound, further structural information is sought through simple chemical transformations or degradative experiments. Reactions which can be conducted on microgram samples, such as ozonolysis, catalytic hydrogenation, acylation, oxidation and reduction, etc., often can confirm the presence of functional groups suggested but not proved by spectroscopic data. In certain cases, it is possible to prove a proposed structure by direct comparison with an authentic sample of the compound, or by partial synthesis from a known natural product.

It should be emphasized that, because there are thousands of compounds in a typical leaf, the bioassay for repellency to the leafcutting ants is critical to the success of each step in the isolation procedure. By the same token, we are assured by the bioassay that every compound so isolated will possess ant repellent properties. Once the compound or compounds are identified, it must still be demonstrated that naturally occuring concentrations of these compounds are repellent to the ants since it is expected that their degree of repellency will be concentration-dependent. It is therefore necessary to estimate the natural concentration of these compounds in the leaf.

Finally, we performed an elemental nitrogen and carbon analysis on leaf tissue samples from the same batches of leaves used in the field leaf preference tests. Assuming that total leaf nitrogen is correlated with total leaf protein as a first order approximation, we can make a preliminary test of the hypothesis that the ants prefer plant species with high-N leaves.

RESULTS

Hypothesis 1 was confirmed : the ants did exhibit continuously graded preferences when presented with a large number of species to choose among. Figure 4 shows the pickup responses of ants from colony 5,16 to leaf disks of 37 plant species in 26 families. Of special interest is that there is a nearly

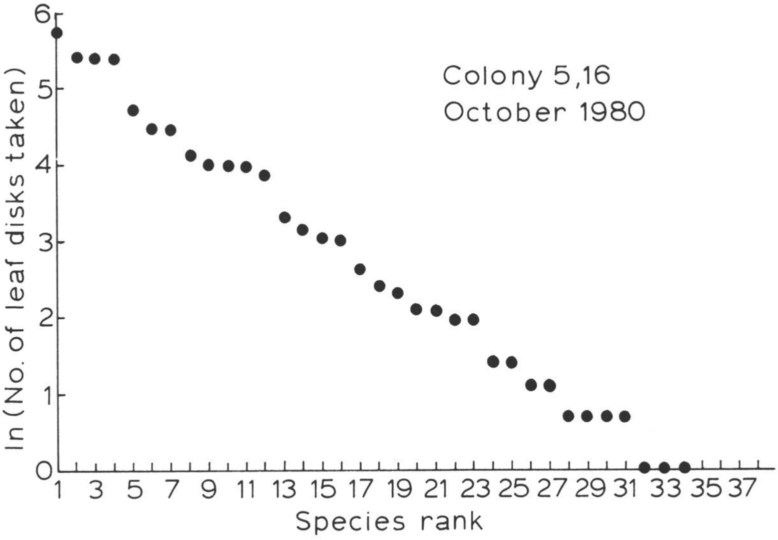

Fig. 4 – Geometric progression of number of leaf disks picked up by colony 5,16 October 1980. Species are ordered in rank from most picked up on the left to least picked up on the right. Species 35-37 were not picked up at all.

Fig. 4 – Progesión geométrica del número de discos de hojas recolectados por la colonia 5,16 en octubre de 1980. Las especies son dispuestas en orden decreciente según como fueron preferidas para la recolección de izquierda a derecha). Ningún disco de las especies 35-37 fué escogido.

perfect geometric series in the relationship between the number of leaf disks taken by the ants and the rank of the species, ordered from most (rank 1) to least (rank 37) preferred. These results show that it is not possible to make a simple partition of plant species into those which are acceptable and those which are unacceptable to the ants, and suggest that there are multiple factors influencing the decision of individual workers to pick up or leave a particular leaf disk.

Hypothesis 2 was partially confirmed : approximately half (11) of the 20 principal test species showed significant seasonal change in acceptability to the ants between July and October (Table 2). Most of the preferred species showed significant seasonal changes in acceptability. A particularly striking case was *Simarouba glauca* which, although almost completely avoided in July, became the fourth most preferred species in October. As a qualitative result, however, most of the preferred species in July remained preferred in October, in spite of quantitative shifts in relative palatabilities. The three preference-test replicates performed on colony 5,16 in October (Table 2) show that, while there is some sample variation, such variation does not obscure the basic pattern of preferences.

Table II – Field leaf preference tests on colony 5,16. Counts are numbers of leaf disks picked up during 1-hour tests in October or July. Three different trails were used for the tests in October, and one trail was used in July. Percentages by species of disks picked up, and binomial contrasts between October and July results, are also shown.

Tabla II – Ensayos de preferencia en el campo sobre la colonia 5,16. Los datos representan el número de discos de hojas colectados durante una hora en octubre o julio. Tres pistas diferentes fueron utilizadas en octubre y una en julio. Son también indicados los porcentajes de discos colectados por especie y los contrastes binomiales entre los resultados de octubre y julio.

	October					July		October - July
Species	1	2	3	Total	%	1	%	Contrasts ($p <$)
Spondias purpurea	138	96	86	320	36.8	51	23.0	.001
Bombacopsis quinata	84	64	76	224	25.8	71	32.0	.05
Bursera simaruba	66	21	24	111	12.8	15	6.8	.01
Simarouba glauca	60	13	14	87	10.0	1	0.5	.0001
Hymenaea courbaril	30	8	15	53	6.1	20	9.0	n.s.
Licania arborea	11	0	3	14	1.6	6	2.7	n.s.
Chlrophora tinctoria	9	14	0	23	2.6	13	5.9	.05
Calycophyllum candidissimum	7	1	0	8	0.9	4	1.8	n.s.
Allophylus occidentalis	6	1	3	10	1.2	2	0.9	n.s.
Exostema mexicanum	5	0	2	7	0.8	1	0.5	n.s.
Hemiangium excelsum	2	0	1	3	0.4	4	1.8	.05
Chomelia spinosa	2	0	0	2	0.2	4	1.8	.01
Annona reticulata	2	0	0	2	0.2	10	4.5	.001
Trichilia cuneata	1	1	0	2	0.2	2	0.9	n.s.
Cordia alliodora	0	0	0	0	0.0	1	0.4	n.s.
Ocotea veraguensis	0	0	1	1	0.2	0	0.0.	n.s.
Manilkara zapota	0	0	0	0	0.0	7	3.1	.001
Piper amalgo	0	0	0	0	0.0	5	2.2.	.001
Malvaviscus arboreus	0	0	2	2	0.2	2	0.9	n.s.
Luehea speciosa	0	0	1	1	0.1	3	1.3	.01

There is also relatively good agreement between different colonies regarding leaf acceptability. Figure 5 compares the October preferences of 3 colonies for the same set of 20 species and individual plants. The species listed across the bottom are ranked from most to least preferred, using colony 5,16 to generate the rankings. Down the right margin of the graph is the cumulative percent of all leaf disks picked up, from highest to lowest ranked species. The top 6 species accounted for 90 % of the leaf disks taken (species above the dotted line) ; and there is nearly perfect agreement between the colonies on the ranking of these species. For the species having preferences below the dotted line, differences between colonies sometimes appear large but for the most part are not statistically significant. Note that these species collectively account for less than 10 % of the leaf disks picked up by the ants.

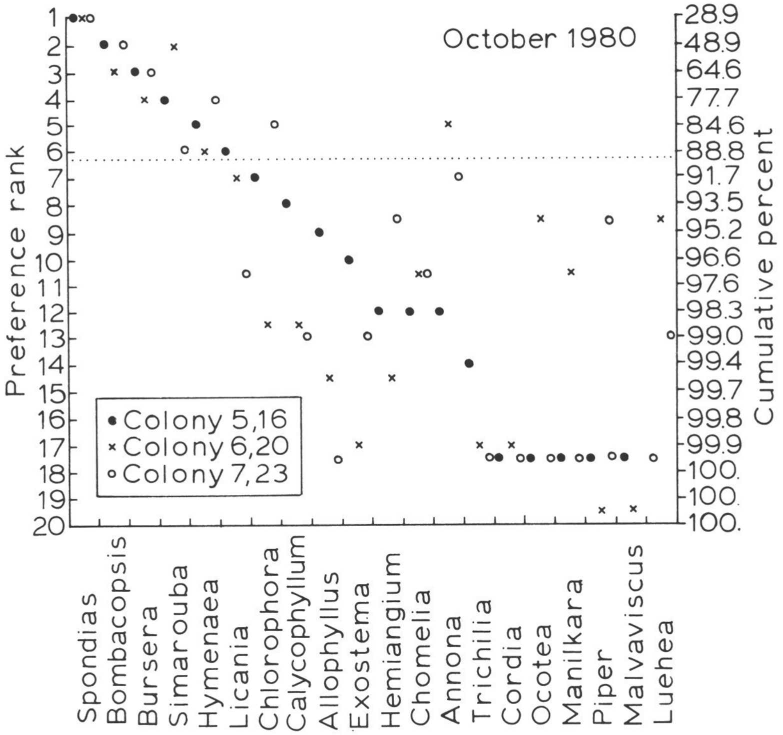

Fig. 5 – Comparison of the preferences of 3 *Atta cephalotes* colonies for the same 20 species and individual plants. Preference ranks were established for colony 5,16 (black dots), and the preference ranks of colonies 6,20 (x's) and 7,23 (open circles) are displayed for comparison of similarities and differences. Along the right margin is shown the cumulative percent of all leaf disks taken, cumulated down from the top-ranked species. Tied preference ranks are shown on the same line.

Fig. 5 – Comparación de las preferencias de 3 colonias de *Atta cephalotes* para las mismas 20 especies o plantas individuales. El grado de preferencia fué establecido para la colonia, 5,16 (puntos negros), y los grados de preferencia de las colonias 6,20 (x's) y 7,23 (circulos abiertos) estan presentados para permitir la comparación de semejanzas y diferencias. A lo largo de la margen derecha se muestran los porcentajes cumulativos de todos los discos de hojas colectados, a partir de la especie de hoja preferida. Los parámetros de preferencia idénticos aparecen en la misma línea.

There are, however, a few significant colony differences for some species (e.g., *Annona purpurea* and *Chlorophora tinctoria*). Since all colonies were offered disks punched from the same leaf samples from the same trees, these differences must be attributed to historical factors, such as the cutting history of the colony. Elsewhere we show that ant preferences can be shifted at least to a modest extent by altering the previous cutting experience of the ants (Hubbell, Stevens, and Wilson, unpubl.).

The preceding results argue that species differences in leaf palatability exist, but it now appears likely that at least some of the observed differences are more of an individual plant effect than a species effect. This conclusion is unavoidable because hypotheses 3 and 4 were also confirmed, namely that the ants can and do discriminate between individual trees, and between leaves from different parts of the same tree. We examined 4 individual > 10 cm in diameter of each of 3 tree species, *Cochlospermum vitifolium* (Cochlospermaceae), *Calycophyllum candidissimum* (Rubiaceae), and *Bursera simaruba* (Burseraceae). The species were chosen because they are known to be attacked by the ants at least for part of the year, and because it was possible to find new and old leaves, and sun and shade leaves, in all combinations on the same tree at one time. Leaf disks of all 4 combinations of young and old, sun and shade leaves of each tree were offered in a simultaneous choice test to the ants. The results for all 3 species were that the leaves of some trees were completely avoided, regardless of the age or light treatment (Table III). If any leaves were taken, in general sunlit leaves were preferred over shade leaves. To

Table III – Preference tests of leaf disks from 4 individuals of 3 tree species. Number of leaf disks picked up in a 1-hour test with simultaneous presentation of each leaf type.

Tabla III – Ensayos de preferencia para discos de hojas de 4 individuos de cada 3 especies de árboles. Número de discos de hojas colectados en 1 hora de bio-ensayo con presentación simultánea de cada tipo de hoja.

		Young leaves		Old leaves		Ind.
Species	Ind.	sun	shade	sun	shade	totals
Cochlospermum	A	0	0	0	0	0
	B	2	0	4	0	6
	C	12	7	5	6	30
	D	0	0	0	0	0
Calycophyllum	A	0	0	0	0	0
	B	3	0	1	0	4
	C	0	1	0	0	1
	D	5	1	2	3	11
Bursera	A	35	4	22	13	74
	B	0	0	0	0	0
	C	2	0	0	0	2
	D	7	7	14	6	34
TOTALS		66	20	48	28	

our surprise, the effect of light treatment appeared to be much stronger than the effect of leaf age.

Hypothesis 5 was not confirmed : the ants do not appear to be selecting leaves which are especially high in nitrogen content. We tested the remainder of the leaf samples which were used in the July field choice tests for total N. Figure 6 shows the lack of relationship between percent nitrogen and the number of leaf disks picked up by ants of colony 5,16 in July. Nitrogen values range from a low of 0,87 % in *Manilkara zapota* to a high of 3,34 % in *Exostema mexicanum*. However, the two species most preferred by the ants, *Spondias purpurea* and *Bombacopsis quinata*, had nitrogen values of 2,30 % and 1,46 %, respectively, right in the middle of the distribution. Although it is still possible that these figures do not accurately reflect the usable protein available to the ants, these results suggest that relative protein content is unlikely to be important in host plant discrimination by these ants. Indeed, a more reasonable hypothesis might be that the ants avoid leaves of either

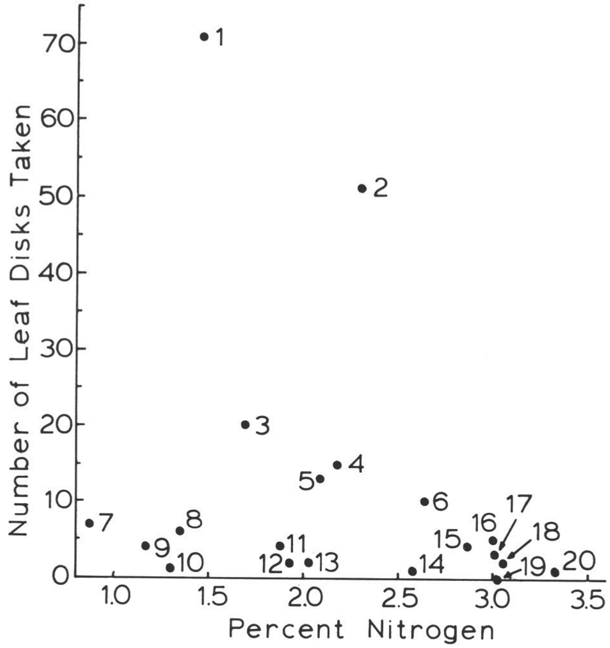

Fig. 6 – Lack of relationship between ant preference and percent nitrogen in leaves of the 20 primary test species. Species 1 is *Bombacopsis* ; species 2 is *Spondias*.

Fig. 6 – Ausencia de relación entre la preferencia de las hormigas y el porcentaje de nitrógeno crudo contenido en las hojas de 20 especies estudiadas. La especie 1 es *Bombacopsis* y la especie 2 es *Spondias*.

extreme : very high or very low N. Resolution of these questions will require study of a much larger number of species, and more accurate assessment of usable leaf protein. As a final comment, we also found no relationship between percent carbon and leaf preference by the ants.

We turn now to our attempts to extract repellent chemicals from the mature leaves of Santa Rosa species avoided by the ants. To date wa have found extractable repellency in 12 out of 18 species we have tested (Table 4). Of particular interest is that most of the chloroform extracts were repellent, whereas most of the ethanol extracts were not. This strongly suggests that most of the ant repellents in these species are nonpolar, lipid soluble molecules such as terpenoids, and not polar compounds such as low molecular weight phenols. Whether this trend is generalizable can only be ascertained from a larger sample of species.

Table IV – Eighteen plant species tested for chemically extractable ant repellency. A (+) indicates significant repellency of crude extracts ($P < 0.05$).

Tabla IV – Diez y ocho especies de plantas probadas para la repelencia de sus extractos. A (+) indica una repelencia significativa de los extractos crudos ($P < 0.05$).

Species	$CHCl_3$	ETOH
Alibertia edulis	−	−
Allophylus occidentalis	+	+
Casearia sylvestris	+	+
Cornutia grandiflora	+	+
Erythroxylon havanense	−	+
Eupatorium morifolium	+	+
Euphorbia schlectendahlii	−	−
Guazuma ulmifolia	−	−
Hemiangium excelsum	−	−
Hymenaea excelsum	+	−
Lasianthea fruticosa	+	−
Luehea speciosa	+	−
Malvaviscus arboreus	+	−
Ocotea veraguensis	+	−
Passiflora slotta	+	+
Pithecollobium saman	−	−
Verbesina gigantea	+	−
Zuelania guidonia	−	−

Using our laboratory bioassay, we have thus far isolated specific ant-repellent compounds from three unrelated species, *Hymenaea courbaril* (Papillionaceae), *Lasianthea fruticosa* (Compositae), and *Ocotea veraguensis* (Lauraceae). We have gone the farthest in the case of *Hymenaea* in that we have demonstrated that the isolated repellent actually functions to repel leafcutting ants in nature. Although the procedures used in isolating and characterizing the repellent in *Hymenaea* leaves are discussed in detail elsewhere (Hubbell, Wiemer, and Adejare, 1983), it is useful to summarize our findings here.

An initial chloroform extract of the leaves was highly repellent, whereas the ethanol extract showed no activity. The activity remained associated with the chloroform solution when this solution was washed with 1.0 N HCl to remove alkaloids and 1.0 N NaOH to remove acids. The material remaining in the neutral fractions was further fractionated by column chromatography, eventually yielding a set of 18 fractions. However, only one of these fractions showed any significant repellency, and that fraction consisted of an essentially pure compound. The ant repellent was identified by GC-MS and ^{1}H and ^{13}C NMR spectroscopy. The spectral data were most consistent with an epoxide derivative of caryophyllene. We confirmed the structure to be caryophyllene epoxide (Fig. 7) by comparison with an authentic sample prepared by partial synthesis.

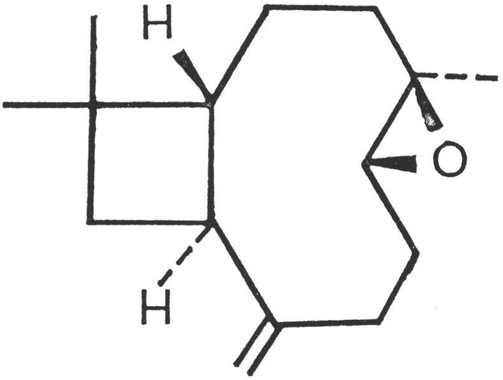

Fig. 7 – Structure of caryophyllene epoxide.

Fig. 7 – Estructura del epóxido de cariofileno.

We estimate the natural concentration of caryophyllene epoxide in *Hymenaea* leaves at approximatively 8 mg/g of leaves (Hubbell, Wiemer, and Adejare, 1983). The laboratory bioassay was then used to measure the repellency of pressed rye flakes treated with caryophyllene epoxide to reflect natural concentrations. Flakes so treated were highly repellent ($p < 0.01$). In contrast, flakes treated with caryophyllene, the precursor to the epoxide, were not significantly more repellent than control flakes, even when tested at concentrations higher than natural levels in *Hymenaea* leaves.

We have also tested the repellency of caryophyllene epoxide under field conditions in Costa Rica. Using the leaf preference bioassay, we demonstrated that leaves of a species normally quite palatable to the ants, *Spondias purpurea*, become nearly as unpalatable as *Hymenaea* leaves when treated with caryophyllene epoxide at the concentration characteristic of *Hymenaea* (Fig. 8). *Spondias* leaves treated with solvent alone were only slightly more repellent than untreated control *Spondias* leaves, so that the effect could clearly be attributed to the caryophyllene epoxide. If the concentration of the epoxide was increased above natural levels, the treated *Spondias* leaves became even more repellent than *Hymenaea*. At concentrations 10 times normal, contact with the chemical produced dramatic changes in ant behavior : the ants jumped or reared back and began intense grooming. These results are convincing evidence that caryophyllene epoxide can and does function in nature as a potent deterrent to leafcutting ant attack in *Hymenaea courbaril*.

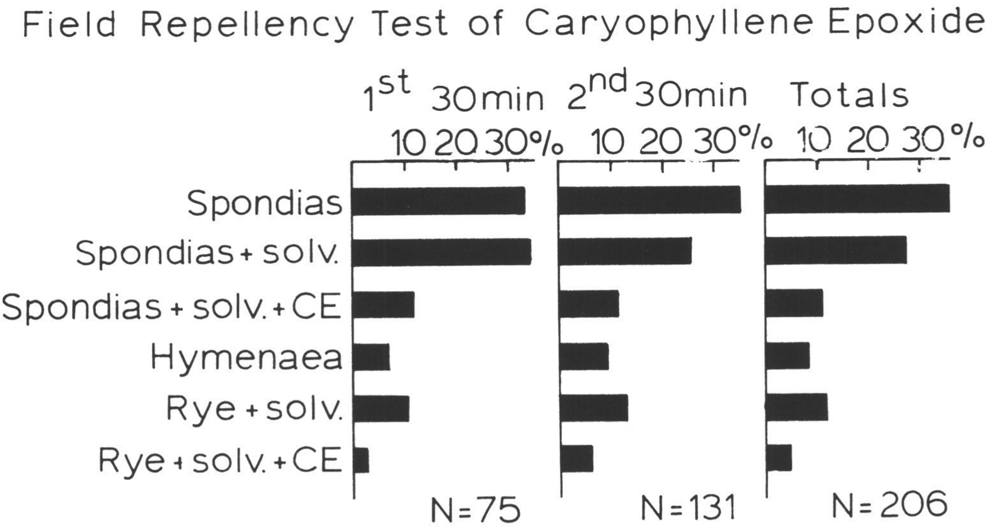

Fig. 8 – Field bioassay of repellency of caryophyllene epoxide (CE). Percentages are the fractions of leaf disks of each treatment picked up in the indicated period.

Fig. 8 – Bioensayo de campo sobre la repelencia del expóxido de cariofileno (CE). Los porcentajes indican las fracciones de discos de hojas recolectados durante el período de tiempo indicado para cada tratamiento.

DISCUSSION

This study has shown that leafcutter ants, when faced with a choice of leaves, are capable of quite finely tuned discrimination of differences in leaf quality. This discrimination operates not only between species, but between individual plants within species, and even between leaves from different parts of individual plants. This may explain why trees in a closed-canopy forest are rarely completely defoliated, and why ants tend to cut only the uppermost, sunlit branches, which presumably have leaves of higher quality.

Because the ants are not required to cut the leaf disks out of leaves in our field leaf preference tests, the ants in making their choices probably rely to a much greater extent on purely chemical cues, rather than on a mixture of chemical and physical cues as would normally be the case. Before picking up a leaf disk, ants always antennated, and nearly always bit, the cut edge of the disk, in behavior most readily interpreted as «tasting». However, this tasting behavior does not put the ant in contact with the chemicals in the leaf for nearly as long as it would take the ant to cut out the disk. If there are slow-acting repellents which only work on relatively prolonged contact, or if the repellents are at lower concentrations where their activity takes more exposure to be expressed, then the pickup bioassay would be expected to overestimate the true palatability of less acceptable species. For example, we suspect that this may have happened in the case of *Hymenaea* in our preference tests : in spite of the presence of known ant repellents, leaf disks of *Hymenaea* were overall sixth in preference. Nonetheless, for our purpose the pickup bioassay is a good conservative screen for finding species which are likely to contain potent ant repellents.

The geometric progression of species ranked by preference was also found by Hubbell and Rockwood (1983) for the leaf material harvested for a month-long period by each of the 20 colonies of *Atta cephalotes* at Santa Rosa. They suggested that the geometric series was actually a small-sample artifact, and showed that if the foraging of a colony were cumulated for an entire year, the distribution became lognormal. They suggested a rather complex model for colony organization wherein such a lognormal could arise, which supposed a colony composed of loosely federated suburbs with semi-autonomous foraging by trail-faithful workers, and a feedback between fungus growth rate and foraging rate for particular plant species.

The present results suggest that a much simpler model of foraging behavior will suffice. These data show that workers on a single trail can also collectively generate the geometric series, and would probably also generate the lognormal if their choices for all 150 + species in the forest were tested. If the same pattern can be seen in a single trail of a colony and does not require pooling over all trails of the colony, then maybe the same behavior is resident in each worker ant as well. Presumably natural selection has fashioned ants capable of discriminating good leaf material from bad as potential substrate for the growth of their fungus.

It should be noted that normally workers do not have a smorgasbord of choices laid out for their choice. The usual situation is that they have walked some tens of meters out from the nest, and a few more tens of meters to the top of a tree, at which point they must make a decision whether to cut or not cut the species, plant, and particular leaf they have encountered. If they choose not to cut, they are forced to search for a longer time to find something acceptable.

It is reasonable to suppose that, as time passes without finding a leaf to cut, the ant's willingness to accept a less palatable species increases. Given the cost of a foraging trip, it would seem better to take some leaf back to the colony, even one of rather inferior quality, than no leaf at all. According to this hypothesis, the distribution of pickup responses in our leaf preference bioassay will be a reflection of the distribution of failure times to find an acceptable leaf to cut. This hypothesis is attractive because it explains the observation in Figure 1, wherein there is a negative relationship between the number of species of leaf disks picked up and trail activity as measured by number of ants returning laden with leaves. It also predicts the observation that the few species which are picked up when there are many laden ants are only those of the highest acceptibility.

We were somewhat surprised to find that the ants paid little attention to the nitrogen content of their leaves. One might have excepted that the ants would be nitrogen (protein) limited and to prefer leaves with high protein content. This may still be true because an elemental nitrogen analysis is only a crude measure of relative protein content. On the other hand, it may also be true that the fungus is sufficiently good at concentrating nitrogen from plant materials that ant choice of species with especially proteinacious leaves is unnecessary. Among fungi, the ant fungus *Rhozites* is very slow growing, suggesting that it may spend considerable metabolic energy in making especially rich dietary substances for the ant larvae.

We were also somewhat surprised at the infrequency which which polar compounds such as small molecular weight phenols have turned up in our bioassay. Because our chemical search for ant repellents is directed by the ants' behavior, there is no particular bias toward finding one particular class of repellent compounds over another. Among students of plant-animal interactions, there is a widespread belief that generalized antimetabolites, such as tannins, are also important anti-herbivore plant defensive compounds (Feeny, 1976 ; Rhoades and Cates, 1976). Data on leaf tannin contents of tree species found in two African forests circumstantially supports this hypothesis (McKey et al., 1978). In one forest growing on nutrient poor soils where leaf production is expensive to the plant, tannin contents are high ; in the other forest, growing on nutrient-rich soils, leaf tannin levels are much lower. Nevertheless, for whatever reason, relatively few tannins have resulted from searches for specific insect antifeedants. In part this may reflect the unwillingness or inability of chemists to characterize these complex polymeric substances. However, in our study to date there has been a genuinely limited role of tannins in the defense of plants against leafcutter ant attack compared to terpenoids. Whether this trend will continue remains to be seen.

One of the most exciting post-result discoveries of this study was the finding that caryophyllene epoxide is a potent fungicide. Not only is it extremely toxic to the ant's own fungus (Hubbell, Wiemer, and Adejare, 1983), but it also kills nearly half of a set of 45 human and plant pathogenic fungi maintened in culture by the Department of Microbiology at the University of Iowa (Cazin, personal communication). Agar media containing as little as 100 μg/ml of caryophyllene epoxide killed 80 % of our *Rhozites* cultures within 48 hours – a concentration only a little more than 1 % of the concentration of caryophyllene epoxide in *Hymenaea* leaves.

Whether plants such as *Hymenaea* have compounds such as caryophyllene epoxide primarily as defenses against fungi or leafcutter ants is not yet known. However, we favor the hypothesis that evergreen species such as *Hymenaea* have probably had a more persistent battle with fungi over their evolutionary history than with leafcutting ants, and that these compounds only incidentally protect *Hymenaea* from ant attack. This hypothesis is supported by the observation that caryophyllene epoxide does not appear to be toxic, or at least strongly toxic, directly to the ants. A test of this hypothesis would be to measure the caryophyllene epoxide concentration of leaves from *Hymenaea* trees growing in Puerto Rico, which has no leafcutting ants.

Further research will reveal whether *Atta cephalotes* has the ability to detect other broad-spectrum fungicides in plants, or wheter the caryophyllene epoxide result was pure coincidence. We strongly suspect, however, that additional ant repellents which we isolate will frequently turn out to have antifungal properties as well.

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THE EFFECTS OF SOME ANT SPECIES, ESPECIALLY ATTA CEPHALOTES (L.), ACROMYRMEX OCTOSPINOSUS (REICH) AND AZTECA SP. (HYM. FORM.) ON CITRUS GROWING IN TRINIDAD

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SUMMARY

Citrus was an important export crop in Trinidad until the rising price of oil made it uneconomic. Citrus farmers controlled two types of ant pests. The leaf-cutting ants *Atta cephalotes* and *Acromyrmex octospinosus* kill both young and old trees by repeatedly defoliating them, and the cultural practices used by the farmers determine which ant species is dominant. The biting ant *Azteca* sp. which builds large arboreal nests on the fruit trees, makes harvesting difficult, and by tending and encouraging homoptera probably reduces fruit yield, and lowers quality by contamination. As *Azteca* sp. and some other ant species deter the leaf-cutting ants from defoliating the mature trees they inhabit, their presence is a mixture of advantage and disadvantage to the farmer. As control using modern toxic baits is simple, farmers aim to control both types of ants.

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RESUMEN

Los efectos de algunas especies de hormigas, especialmente Atta cephalotes **(L.),** Acromyrmex octospinosus **(Reich)** y Azteca **sp. en Trinidad**

Los cítricos fueron un importante cultivo de exportación en Trinidad, hasta que el alza en el precio del petróleo los hiciera incosteable. Los cultivadores de cítricos controlaban dos tipos de plagas de hormigas : las hormigas defoliadoras *Atta cephalotes* y *Acromyrmex octospinosus* que matan tanto los árboles jóvenes como los adultos defoliándolos repetidamente. Las prácticas de cultivo usadas por los agricultores determinan cuál de las especies de hormiga es dominante. Las hormigas mordedoras *Azteca* sp., las cuales construyen grandes nidos arbóreos en los árboles frutales, hacen difícil la cosecha, y por el cuidado y fortalecimiento de Homóptera, probablemente reducen la cosecha de fruta, y disminuyen la calidad por contaminación. Mientras que *Azteca* sp. y algunas otras especies de hormigas impiden la defoleación de los árboles que habitan, su presencia para los agricultores es una mezcla de ventajas y desventajas. Como el control usando cebos tóxicos modernos es simple, el objectivo de los agricultores es controlar ambos tipos de hormigas.

INTRODUCTION

Citrus, (oranges, grapefruit and limes) have been grown commercially in Trinidad for many years, and in the early sixties some 5500 ha were planted, yielding 48,000 tons for export and earning TT$ 7.8 million, making it the third most important export crop in the island (Maliphant, 1966 ; Lewis and Norton, 1973). With the rise in the price of oil in the seventies however, the economy of Trinidad which is an oil-rich country, underwent profound changes, the cost of labour to work the plantations became increasingly uneconomic, and the citrus industry went into decline, so that by the late seventies, Trinidad was importing citrus juice concentrates for home consumption.

Studies in Trinidad on the impact of the leaf-cutting ants *Atta cephalotes* (L.) and *Acromyrmex octospinosus* (Reich) on citrus have been carried out since 1966 (Cherrett, 1968a ; Cherrett & Sims, 1968 ; Cherrett & Merrett, 1969 ; Lewis & Norton, 1973 ; Cherrett & Lewis, 1974 ; Lewis, 1975), and these changes in the fortunes of the citrus industry made it possible to compare ant faunas and their impact in managed orchards, and in abandoned ones. This has provided valuable insights into their effects.

Citrus growers in Trinidad recognise the need to control two types of ant pests, – leaf-cutting ants (Bachacs) and *Azteca* sp. (Biting ants). The effects of these will be examined in turn.

EFFECTS OF LEAF-CUTTING ANTS

Only two species of leaf-cutting, fungus-growing ants are found in Trinidad (Cherrett, 1968a) the forest bachac *A. cephalotes*, which builds large nests up to 250 m^2 in surface area, containing several million ants, and the garden bachac *A. octospinosus*, which builds much smaller nests only one or two square metres in surface area and containing fewer than 10,000 ants (Lewis, 1975). Assessing their economic importance in managed citrus estates, Cherrett and Sims (1968) estimated a mean annual loss, including the cost of control measures of TT$ 49 ha^{-1} and Lewis and Norton (1973) gave a figure of TT$ 29 ha^{-1}. In both cases the figures were based on farmers' estimates of losses to newly-planted citrus saplings of 30 % and 16 % respectively. Neither study took any account of the effects of defoliation on mature trees, which Cherrett and Lewis (1974) regarded as trivial on trees older than 5 years. As all their studies were conducted in orchards where vigorous leaf-cutting ant control was practiced, the significance and the economics of control could only be assessed in the context of the losses still experienced despite these control measures.

Jutsum el al. (1981) however, studied a citrus orchard abandoned in 1972, and in 1976 they noted that 20 of the 108 trees examined (19 %) were dead. Because broad trails of *A. cephalotes* were common throughout the area, and because 27 of the 88 living tress were at least 50 % defoliated, they concluded that the dead trees had been killed through repeated defoliation by ants. During a visit in 1979, the original surveyed area was difficult to distinguish, as the dead trees had disappeared. However in an area considerably larger, only 40 living citrus trees could be found. This illustrates why farmers practice leaf-cutting ant control even in mature orchards because in many areas citrus culture would be impossible without it. This was confirmed by farmers around Bartica in Guyana who were questioned in 1963 about the shortage of citrus fruit. They claimed that citrus was not worth growing there because of leaf-cutting ants.

The species causing most damage in Trinidad depends upon whether or not control measures are carried out (Cherrett, 1968a ; 1981). With control, *A. octospinosus* which reproduces more rapidly and has inconspicuous nests is favoured (Table I). It reaches worker ant densities of 28 m^{-2} and nest densities of 36 nests ha^{-1} (Lewis, 1975). The large nests of *A. cephalotes* however are readily detected and killed. In the abandoned orchard without control, only three *A. octospinosus* nests were seen, and *A. cephalotes* appeared to be regaining the dominance it possesses in tropical rain forests where, with 0.6 nests ha^{-1} (Cherrett, 1968a), the worker ant density may be about 180 m^{-2}. This species difference between forest and cultivated land is in part

Table I – A comparison of the leaf-cutting ant faunas of tropical rain forest and nearby cultivated or cleared land (modified from Cherrett 1968a).

Tabla I – Comparación de las faunas de hormigas defoliadoras entre la selva tropical y las cercanas de las áreas abiertas o cultivadas.

	Cultivated or cleared land		Forest		
	Atta cephalotes	*Acromyrmex octospinosus*	*Atta cephalotes*	*Acromyrmex octospinosus*	Significance (P) of the difference *
Number of nests in 8 ha	3	21	5	0	<0.001
Number of founding queens caught in 20 pitfall traps during 15 months	2	30	9	0	<0.001

* Using a Fisher exact test on a 2 x 2 contingency table

due to the settling preferences of the flying queens when seeking a nest site (Table I), but it is not known if the species shift between cultivated and abandoned citrus estates is assisted by hostile interactions. In the field, both species show intraspecific aggression (Jutsum et al., 1979), although interspecific aggression could only be demonstrated if workers of one species were placed very close to the nest entrance of the other (Jutsum, 1979).

EFFECTS OF *AZTECA* SP.

The most obvious arboreal-nesting ant found in Trinidad citrus orchards is a species of *Azteca* building large dark-brown carton nests shaped like an inverted cone, which hang from the trunk and larger branches. As the genus is in need of revision, specific identification was not considered possible (B. Bolton, W.L. Brown Jr., personal communications). The species is polydomous, one colony making a series of carton nests in nearby trees (Jutsum et al. 1981). The number of nests in infested citrus trees in 1976 is shown in Table II.

Table II – The number of large nests of *Azteca* sp. found in eighty-eight citrus trees surveyed in 1976.

Tabla II – Número de nidos grandes de *Azteca* sp. encontrados en ochenta y ocho cítricos monitoreados en 1976.

Number of nests per tree	0	1	2	3	4	5	6	7	8	>8
Number of trees	51	10	4	3	2	3	2	1	2	10

In a well-maintained citrus estate, only one tree in a hundred contained an *Azteca* sp. nest, whilst in the abandoned orchard, part in a steep-sided enclosed valley, had only one tree in thirty-four (3 %) with a nest. In the main study area however, on a more open sunny site, thirty-seven out of eighty-eight living trees (42 %) possessed nests in 1976 with an increase to forty-six out of seventy-nine (58 %) in 1977.

Azteca sp. is predatory (it will feed readily on liver baits) ; saccharophilic (it tends scale insects and builds carton shelters over some species) , possesses several static nests, and is arboreal. Leston (1973) has listed all of these as characteristic of dominant ants in a mosaic. As a consequence, *Azteca* sp. has a profound influence on the fauna of the trees it inhabits. Jutsum et al. (1981) found that citrus trees with *Azteca* sp. were much more likely to be infested with the soft green scale *Coccus viridis* (Green), and a stem-living coccid *Toumeyella* sp. n. normally found under protective shelters built by the *Azteca* sp. workers. They also has substantial quantities of sooty moulds (Erysiphales) on their leaves, giving the whole tree a black appearance (Table III). There was evidence that the arboreal-nesting termite *Nasutitermes costalis* Holmgren was not found on trees occupied by *Azteca* sp., and an indication (not statistically significant as very small numbers were involved) that a polybiine wasp (possibly *Polybia rejecta* (Fab.)) was positively associated with the ant.

Table III – The influence of *Azteca* sp. on the fauna and flora of citrus trees (modified from Jutsum et al., 1981).

Tabla III – Influencia de *Azteca* sp. sobre la fauna y la flora de cítricos (modificado de : Jutsum et al., 1981).

	Percentage of all the trees examined (n) with the organisms present		Significance (P) of the difference *
	Trees with *Azteca* sp.	Trees without *Azteca* sp.	
Nests of wasp (*Polybia* sp.)	11(37)	2(51)	>0.05
Nests of termite (*Nasutitermes costalis*)	0(37)	18(51)	<0.01
Soft green scale (*Coccus viridis*)	80(20)	20(10)	<0.01
Stem coccid (*Toumeyella* sp.n)	65(20)	0(10)	0.001
Sooty moulds (*Erysiphales*)	95(20)	10(10)	<0.001

* Using a Fisher exact test on a 2 x 2 contingency table

Farmers regard *Azteca* sp. as a pest, primarily because the workers are aggressive and bite if the tree is disturbed. This impedes harvesting the fruit. *Polybia* nests are especially feared by farm workers and if the association with *Azteca*, suggested by Kirkpatrick (1957) is confirmed, it would be regarded as a further disadvantage of *Azteca* sp. The effects of the enhanced numbers of scale insects have not been quantified, but yield is almost certainly reduced. Rai (1977) showed that *Azteca* sp. on coconuts in Guyana increased the incidence of the coconut scale *Aspidiotus destructor* Sign., and the mealybug *Nipaecoccus nipae* (Mask) and reduced the yield of nuts by 62 %. Contamination of citrus fruit by scales and sooty mould growth lowers its market value. As a result, farmers usually control *Azteca* sp. numbers by a combination of cutting down and spraying their nests.

However, the effects of *Azteca* sp. are not all deleterious. Vello (1971) recorded increased pollination in cocoa trees inhabited by *Azteca chartifex spitini* Forel, although the mechanism by which pollinating insects are attracted is not clear, and Eberhard and Kafury (1974) showed that the arboreal-nesting *Azteca trigona* was a possible defence against leaf-cutting ant attack.

INTERACTIONS BETWEEN ANT SPECIES

Leston (1973) working in Africa pointed out that the dominant ant species occupy different individual trees, and so form a mosaic in tree crops and forests. As the dominants are mutually exclusive, the other insect species associated with them may also form a mosaic. Leston (1978) extending his studies to the Neotropics, showed that in natural forest, *Dolichoderus attelaboides* (Fabricius) chemically repulsed individuals of *A. cephalotes* or physically removed them from the trunk.

Jutsum et al. (1981) noted that the incidence of defoliation by *A. cephalotes* in the abandoned citrus orchard was very patchy. Trees without *Azteca* sp. or either of the other two dominants, *Crematogaster brevispinosa* Mayr and *Dolichoderus bidens* L. had an average 54 % foliage loss in 1977 whilst those with *Azteca* sp. suffered only à 5 % loss. They observed *Azteca* sp. and *C. brevispinosa* attacking isolated *A. cephalotes* workers (presumably scouts seeking new sources of leaves) which had wandered on to the trunks of the trees they inhabited. On trees otherwise completely defoliated by *A. cephalotes*, they also noted that branches in the immediate vicinity of the small felt and leaf nests of *D. bidens* were fully foliated and bore flowers and fruit, and they surmised that this must be due to aggression towards the leaf-cutters. A survey of ten trees without *Azteca* sp. revealed one with *C. brevispinosa* and two with *D. bidens.*

The role of *Azteca* sp. in preventing *A. cephalotes* defoliation was demonstrated experimentally (Jutsum et al., 1981). Nineteen trees with *Azteca* sp. nests were treated with a toxic bait made from ground liver using Mirex (dodecachlorooctahydro-1,3,4-metheno-2H-cyclobuta (cd) pentalene) as the toxicant, and ten untreated trees with *Azteca* sp. were left as controls. Within twenty-five days, *Azteca* sp. activity had ceased on all nineteen trees, there being no living ants in the nests. On only one of the ten untreated trees was the *Azteca* sp. killed, and this was due to their foraging on a nearby baited tree. One tree was defoliated by *A. cephalotes* only 72 h after baiting, the leaf-cutter workers standing in apparently aggressive attitudes beside the carton shelters still housing the dying *Azteca* sp. workers. By the end of the observation periods (a maximum of 33 days), fifteen trees (79 %) had been attacked by *A. cephalotes*, compared with only one (10 %) of the untreated control trees patrolled by living *Azteca* sp.

Following the death of the *Azteca* sp. on the baited trees, the majority of the *Coccus viridis* and *Toumeyella* sp. n. scales died within a month. This was associated with an increase in the numbers of larvae of a coccinellid predator *Azya*, a probable increase in fungus disease on *C. viridis*, and the disintegration of the carton shelters built over the dead *Toumeyella* sp. n. by *Azteca* sp.

CONCLUSIONS

It is clearly established that *Azteca* sp. can inhibit the defoliating activities of *A. cephalotes* on the citrus trees it occupies. However, some leaf-cutting does occur even on *Azteca* sp. inhabited trees. This may be due to *A. cephalotes* workers gaining access to the tree where it touches another, or via a liane, so allowing cutting to occur well away from the *Azteca* sp. nest without the leaf-cutters having to climb up the normally well-defended trunk. The observation that *A. cephalotes* invaded trees before all the *Azteca* sp. had died, suggests that when numerically superior, they may be able to inhibit *Azteca* sp. attack. The continuing tree death in the abandoned orchard from 1972 to 1979, probably from leaf-cutting ant defoliation suggests a progressive breakdown in *Azteca* sp. defence. As *Azteca* sp. is polydomous, it may only require a temporary withdrawal of workers from one tree, or a failure of one satellite nest, to permit that tree to be defoliated. As defoliation removes all the *C. viridis*, the tree will become less attractive to the *Azteca* sp. so lessening the vigour of its defence and permitting further defoliations. This may cause *Azteca* sp. to abandon the tree before it is killed by repeated defoliation.

As *Azteca* sp. nests are not normally encountered on small citrus trees, they do not provide any protection to newly-planted, saplings, the most vulnerable stage in citrus culture. Because they bite, and encourage such high populations of homoptera, *Azteca* sp. is not likely to be acceptable to farmers as a competitive displacement agent for the biological control of leafcutting ant damage. *D. bidens* is effective over such a short distance from its nest that acceptable sized populations would not provide control, but *C. brevispinosa* might repay closer study to see how effective it is, and what are its disadvantageous side effects.

For the present, citrus growers in Trinidad like to keep their trees free of both *Azteca* sp. and leaf-cutting ant damage. By using toxic baits this can be done simply, cheaply and with minimum toxic hazard to the environment (Lewis, 1973 ; Lewis & Phillips, 1973 ; Jutsum et al., 1981).The use of arboreal-nesting dominant ants to control leafcutting ant damage in forestry may be more promising as the disadvantages of biting ants disrupting harvesting operations, or of enhanced homoptera populations reducing yield and contaminating the crop may be less important. However the effectiveness of defensive ants in limiting leaf-cutting ant damage in tropical forests is far from clear. Leston (1978) found lacunae in the defence of a forest stand in Brazil, and if a large proportion of trees are normally undefended, then Cherrett's (1968b) explanation of why the ants travel so far from the nest to cut trees, namely that they are adopting a conservational grazing system to even out the rate of exploitation over their territory, may still be valid. Some of the large grass-cutting ants such as *Atta vollenweideri* For. and *Atta capiguara* Gonçalves seem to adopt a similar foraging pattern, although a mosaic is unlikely to be operating. If many trees in natural forest are undefended, the reasons for this may make it difficult for man to increase (as a biological control) the proportion defended in his plantations. This is an area where more research is needed.

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CHEMICAL COMMUNICATION SYSTEMS IN THE ANT ATTA CEPHALOTES

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SUMMARY

Leaf-cutting ants have elaborate chemical communication systems. They communicate alarm with a pheromone from the mandibular gland ; use a trail pheromone to orientate nestmates to the food source and to inform them about the quality of the food they are recruited to ; mark their territory with the secretions of the valve glands ; and have many exocrine glands with a possible role in chemical communication. *Atta cephalotes* recognise workers from another species (*Acromyrmex octospinosus* and *Atta sexdens*) and from other colonies of its own species as aliens. Species-specific recognition appears to be based on volatile substances on the cuticle, probably produced by the mandibular glands. There is some evidence that colony-specific recognition rests on detection of colony differences in the composition of the cephalic alarm pheromone. These ants dispose of waste products from the nest in a way different from that in which they dispose of wastes of other origins. The process of dumping refuse seems to involve a different programme of behaviour from that used for collection of food, although no caste-specificity in this behaviour could be detected. Chemical signals are used to recognise the wastes originating from the nest.

RESUMEN

Los sistemas de comunicación química en la hormiga *Atta cephalotes*

Las hormigas del género *Atta* tienen varios sistemas de comunicación química. Ellas comunican alarma con una feromona proveniente de la glándula mandibular ; usan una feromona de camino para orientar a las compañeras a la fuente de alimento y para informarlas acerca de la calidad del alimento ; marcan su territorio con la secreción de las glándulas de los palpos del aguijón ; y tienen varias glándulas exocrinas más con una posible función en comunicación química. *Atta cephalotes* reconoce a obreras de otras especies (*Acromyrmex octospinosus* y *Atta sexdens*) y de otras colonias de su misma especie como extrañas. El reconocimiento especie-específico parece posible gracias a sustancias volátiles en la cutícula, probablemente provenientes de la glándula mandibular. Hay evidencias de que el reconocimiento específico para cada colonia de *A. cephalotes* se logra gracias a la capacidad de estas hormigas de detectar diferencias en las proporciones relativas de los componentes de la feromona de alarma. Estas hormigas disponen de los desechos del nido de forma diferente a como disponen de desechos de otro origen. Parece existir un programa comportamental específico para botar los desechos del nido en el sitio específico que tiene la colonia para ello. No se pudo observar una especificidad de una de las castas por ese comportamiento. Señales químicas le sirven a estas hormigas para reconocer los desechos del nido.

INTRODUCTION

The communication systems of the leaf-cutting ants from the genus *Atta* are complex and could be classified among the most evolved in the Hymenoptera. Various different exocrine glands have been described in workers of these ants (Fig. 1). For some of them a function in communication is known, but for others not. It is to expect that eventually a function in communication for most of these glands are found. Thus, the mandibular gland secretes a multiple function alarm pheromone, which is used to attract nestmates and to direct the attack to the source of disruption (Crew and Blum, 1972). The same pheromone seems to be used to recognize the individuals from the same colony as we shall see later, and possibly is also used as the colony specific component in territorial recognition (Jaffé et al., 1979). The valve glands (Bazire-B and Zylberberg, 1979) are used for marking the territory at least with the species-specific component (Jaffé et al., 1979). The poison gland is used by these ants for chemical mass recruitment to the food source (Moser and Blum, 1963). It orientates the workers to the food source, giving spatial information, and at the same time it gives information about the quality of the food (Jaffé and Howse, 1979, and Jaffé, 1980). The mayor component of this pheromone, the methyl-4-methylpyrrole-2-carboxylate has two different effects on the ants. If applied as a trail at concentrations down to 10^{-14} gr/cm it produces its known orientation effect. At higher concentrations (about 5×10^{-11} gr/cm or more) it works as an attractant. This double effect is used by the individual ant to modulate the amount of recruitment required to exploit the food source. The function in communication of the other exocrine glands is still unknown. These ants also use pheromones or chemical substances for recognizing the waste products from the nest and thus take them to the refuse deposit, as will be described below. They recognize their brood with the help of an unknown chemical signal (Robinson and Cherrett, 1974) and probably also use pheromone for sex attraction. Inside the nest, communication for the coordinate building of the galleries, the recognition of castes, of the fungus, etc., are very probably also due to the help of chemical signals.

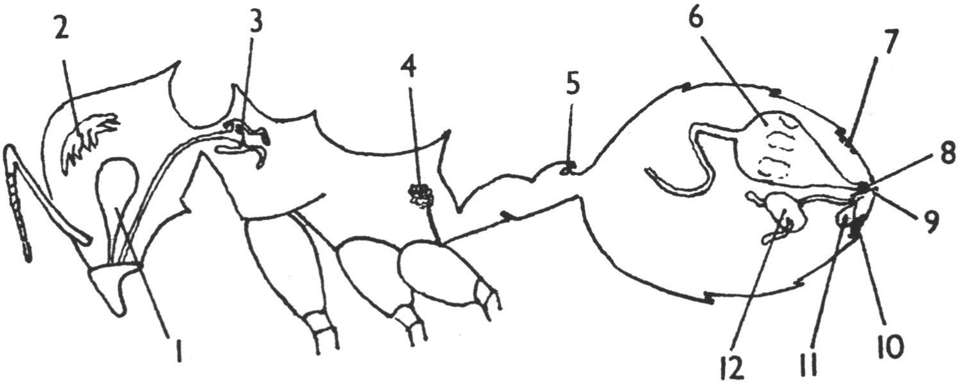

Fig. 1 – Exocrine glands of *Atta cephalotes* and its known function. 1 – Mandibular gland (alarm, individual recognition and probably also territorial marking) ; 2 – Postpharyngeal gland ; 3 – Salivary gland ; 4 – Metapleural gland (produces antibiotics) ; 5 – Stridulatory apparatus (ultasound production) ; 6 – Rectal sac , 7 – Tergal gland ; 8 – Valve glands (territorial marking) ; 9 – Sting ; 10 – Sternal gland (defence secretions) ; 11 – Dufour's gland ; 12 – Poison gland (orientation along a trail, information about the quality of the food).

Fig. 1 – Glándulas exócrina de *Atta cephalotes* y sus funciones conocidas. 1 – Glándula mandibular (alarma, reconocimiento individual y probablemente también marcaje territorial) ; 2 – Glándula postfaringal ; 3 – Glándula salivar ; 4 – Glándula metapleural (produce antibióticos) ; 5 – Aparato estridulador (produce ultrasonido) ; 6 – Saco rectal ; 7 – Glándula tergal ; 8 – Glándulas de los palpos del aguijón (marcaje territorial) ; 9 – Aguijón ; 10 – Glándula esternal (secreción de defensa) ; 11 – Glándula de Dufour ; 12 – Glándula de veneno (orientación en caminos, información sobre la calidad del alimento).

RECOGNITION OF NESTMATES

Materials and methods

Tests were carried out in the laboratory on nest tables of *Atta cephalotes* colonies at Southampton University, England. Ants were killed by plunging them into finely crushed dry-ice. Dead ants were used in experiments after the body temperature equilibrated with the room temperature. Freeze-drying was carried out after killing the ants as just described, using a vacuum pump and a refrigerated supporting plate. Pressures of about 0.5 x 10^{-3} mm Hg at - 40°C during 12 hours were applied to the ants during the process. Impregnated freeze-dried ants were those freeze-dried ants which were placed in a small closed plastic cup together with two crushed heads, thoraxes or gasters, for 5 minutes. Gas chromatography on 5 % Carbowax columns together with the solid sample technique (Morgan and Wadhams, 1972) was used for studying the relative amounts of the alarm pheromone components of *A. cephalotes*. 4-Methyl-3-heptanone was identified by assuming it to be the major component of *A. cephalotes* head volatiles (Riley et al., 1974a). 2-Heptanone was identified by co-injection with the synthetic compound using the Carbowax columns.

RESULTS

General observations

Test ants were placed on an *Atta cephalotes* nest table and the reaction of the workers of the host colony was observed. An ant from the same colony was examined briefly with the antennae of the workers after being placed on the table, and then entered the nest. An ant of the same species, but from a different colony was attacked. The foreign ant, as soon as it was placed on the table showed alarm behaviour, probably due to the presence of a colony-specific territorial pheromone. The workers attacked the alien ant until it jumped from the table or until it was killed. The same was observed when an ant from a different species (*A. sexdens* or *Acromyrmex octospinosus*) was placed on the nest table ; in this case, the attack was more violent and the workers of the host colony seemed to detect and find the alien ant much faster. In all three cases, alarm behaviour was elicited in the host colony. If the same kind of ant were anaesthetised with carbon dioxide and then placed on an *A. cephalotes* nest table, different responses from the host colony were observed. The workers attacked only the ant of a different species, which was sometimes dropped over the edge of the table before it recovered. Both kinds of *A. cephalotes* ants were examined extensively with the antennae, and the workers attacked the ant from a different colony only when it recovered.

When the three type of ants, killed with dry-ice, were presented on the *A. cephalotes* nest table, behaviour similar to that with anaesthetised ants could be observed. All three types of ants were eventually dropped over the edge of the table, but only the ant from a different species (*Acromyrmex octospinosus*) elicited aggression from the workers. *A. cephalotes* workers were not attacked, even if they came from a different colony. The time the dead ants remained on the nest table before they were picked up and dropped off the table (Table I) was less for dead *Acromyrmex* than for dead *A. cephalotes* workers. Freeze-dried ants, when presented to an *A. cephalotes* colony were very soon picked up and dropped off the edge of the table (Table I). No attack or extensive examination by the workers could be observed with any of the freeze-dried ants.

Table I – Mean and standard deviation of the time (min) an ant remains on the nest table of an *A. cephalotes* nest before it is picked up and dropped off the edge of the table (n = 8).

Tabla I – Media y desviación estandard del tiempo (min) que una hormiga permanece sobre el nido de una colonia de *A. cephalotes* antes de ser recogida y botada fuera del mismo (n = 8).

Form of presentation	Ants from same colony	Ants from different colony	Ants from different species (*Acromyrmex octospinosus*)
Dead	25.3 ± 12.1 a	24.1 ± 10.7 a	5.2 ± 2.8 b
Freeze-dried	0.6 ± 0.5 c	0.7 ± 0.3 c	0.8 ± 0.3 c

a, b, and c indicate statistically different means ($p < 0.05$) by Hartley's test (ANOVA, F = 25.4, $p < 0.001$)

These observations show that ants from different species are recognised even if dead ; but ants from different colonies of the same species are recognised as such only if they are alive and active. The experiment with freeze-dried ants suggets that the species recognition signal is a volatile chemical.

The odour source for species recognition

Body parts of freshly-killed *A. cephalotes* and *Acromyrmex octospinosus* workers were presented to an *A. cephalotes* colony. The body parts, head, thorax and gaster, were examined by the ants of the host colony for different lengths of time (Table II) before they were picked up and dropped off the edge of the table. All the body parts of *A. cephalotes* were examined for a longer period than those of *Acromyrmex octospinosus*, although all came from a colony different to the host colony, which suggests the presence of a chemical cue all over the body, probably on the cuticle, which is used in species recognition. When body parts of freeze-dried *A. cephalotes* ants were presented to an *A. cephalotes* colony, none were examined for long but were dropped off the table immediately, which again suggests a volatile chemical cue, acting as the species recognition signal. All body parts were examined for a much shorter period if freeze-dried, with the exception of the gaster, in comparison with the body part of a freshly-killed ant (Table II).

Table II – Mean time and standard deviation (min) for which different body parts of freshly-killed ants from two different species remained on the nest table of an *A. cephalotes* nest before they were picked up and dropped off the table (n = 6).

Tabla II – Media y desviación estandard del tiempo (min) que diferentes partes del cuerpo de una hormiga recien muerta de dos especies diferentes permanece sobre el nido de una colonia de *A. cephalotes* antes de ser recogida y botada fuera del mismo (n = 6).

Species	Body part examined : Head	Thorax	Gaster
A. cephalotes	11.4 ± 3.3 bd	12.6 ± 11.6 bd	6.1 ± 7.1 cd
Acromyrmex octospinosus	2.7 ± 1.6 c	4.3 ± 3.5 c	1.0 ± 0.6 a
Freeze-dried *A. cephalotes*	0.6 ± 0.2 a	0.8 ± 0.3 a	1.3 ± 0.7 ac

a, b, c, and d indicate statistically different means ($p < 0.05$) by Students t-test (ANOVA, F = 5.77, $p < 0.001$)

When freeze-dried *A. cephalotes* workers were impregnated with the odours from crushed body parts of *A. cephalotes* from a different colony and of *Acromyrmex octospinosus* workers, and were then presented to an *A. cephalotes* colony, different «pick-up» times were observed (Table III). Freeze-dried ants, impregnated with odours from the heads of either *A. cephalotes* or *Acromyrmex octospinosus* were examined for a longer period than those impregnated with odours from the thorax and gaster. No difference between either species could be detected in this experiment (Table III).

Table III – Mean time and standard deviation (min) a freeze-dried *A. cephalotes* ant, impregnated with vapors from crushed body parts from two different species, remained on an *A. cephalotes* nest table before it was picked up and dumped off the table (n = 6).

Tabla III – Media y desviación estandard del tiempo (min) que una hormiga liofilizada de *A. cephalotes*, impregnada con vapores de diferentes partes del cuerpo de hormigas de dos especies diferentes, permanece sobre el nido de una colonia de *A. cephalotes* antes de ser recogida y botada fuera del mismo (n = 6).

Species	Body part examined : Head	Thorax	Gaster
A. cephalotes	4.2 ± 2.3 b	0.8 ± 0.6 a	0.8 ± 0.3 a
Acromyrmex octospinosus	4.5 ± 1.2 b	1.3 ± 1.2 a	1.6 ± 1.2 a

a and b indicate the means which are statistically different ($p < 0.05$) using the Hartley's test (ANOVA, F = 6.83, $p < 0.001$)

These experiments suggest that the species-specific recognition signal is a volatile compound or mixture of compounds over all the cuticle of the ant. The source of this volatile seems to be the head.

The colony-specific recognition of individuals

Colony-specific recognition is achieved only if the test ant presented is alive and active. Therefore, the different body parts : head, gaster and thorax ; were cut off grom live *A. cephalotes* workers from different colonies and were presented to an *A. cephalotes* colony (Table IV). No significant difference could be observed between body parts from ants of the same colony and from different colonies. In this experiment, thoraces with their legs removed were used for the test. The reason is that the legs can easily be grasped by the workers and a thorax with legs is therefore sometimes picked up by more than one ant, which results in pulling and competing for the same body part, which then will give unrealistic pick-up times for the thorax. If, instead of small body parts, more complete parts of an ant were presented to the colony, different results were obtained (Table IV). Ants with their legs and gaster removed were picked up and dropped off the table much faster if they came from different colonies of the same species than if they were from the same colony. Headless ants with or without legs were not examined extensively or attacked, in spite of the fact that they were showing movements similar to those of ants with head, but they remained on the nest table for several hours, whichever colony they originated from. Ants with only their feet removed, were attacked and dropped off the table much faster if they came from a different colony (Table IV).

Table IV – Mean time and standard deviation (min) for which a body part of a live *A. cephalotes* ant remains on the nest table of a colony of the same species before it is picked up and dropped off the table (n = 6).

Tabla IV – Media y desviación estandard del tiempo (min) que partes de una hormiga viva de *A. cephalotes* permanece sobre un nido de una colonia de su misma especie antes de ser recogida y botada fuera del mismo (n = 6).

Body part tested	Ant from same colony	Ant from different colony	Probability (t-test)
Head	12.9 ± 5.6	11.0 ± 8.5	>0.1
Thorax without legs	7.8 ± 7.2	3.2 ± 4.5	>0.1
Gaster	11.4 ± 10.5	12.9 ± 8.7	>0.1
Head and thorax without legs	9.5 ± 3.6	2.4 ± 2.0	<0.05
Head, thorax and gaster without legs	14.6 ± 7.9	4.9 ± 4.2	<0.05
Thorax and gaster without legs	11.2 ± 6.0	10.5 ± 3.7	>0.1
Thorax with legs and gaster	>60	>60	–

The results suggest that the colony-specific recognition of *A. cephalotes* workers is due to some signals from the head which are not present in isolated heads. These signals are probably volatile compounds from the head together with some kind of movement which is absent in isolated heads.

Colony differences in head volatiles

Gas chromatograms of heads of workers from different colonies show the same compounds but in different proportions (Fig. 2). Analysis of the amount of the major components of head volatiles from young media workers showed that at least the relative amounts of 4-methyl-3-heptanone and 2-heptanone are more or less constant between of the same colony but different between colonies of *A. cephalotes* (Table V). The four colonies examined were fed and cared for in an identical way for over 3 years.

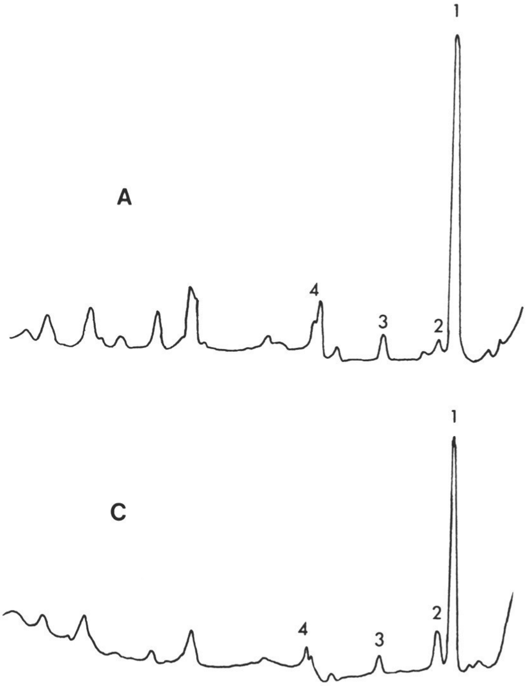

Fig. 2 –Solid-sample gas chromatograms of the head of one *Atta cephalotes* media worker, on a 5 % Carbowax column. Trace reads from right to left ; temperature program : 4° per min increase from 70° to 190°C. A and C indicate the colony of origin. 1 is 4-methyl-3-heptanone, 2 is 2-heptanone, 3 and 4 are probably 3-octanone and 3-octanol respectively.

Fig. 2 – Cromatógramas de muestras solidas gasificadas de cabezas individuales de obreras medias de *Atta cephalotes*, usando columnas de Carbowax al 5 %. El gráfico se lee de derecha a izquierda ; programa de temperatura : incremento de 4° por min de 70° a 190°C. A y C indican la colonia de origen. 1 es 4-metilo-3-heptanona, 2 es 2-heptanona, 3 y 4 son probablemente 3-octanona y 3-octanol respectivamente.

Table V – Ratio between peak areas of 4-methyl-3-heptanone and 2-heptanone in gas chromatograms of *A. cephalotes* media workers heads.

Tabla V – Relación entre las áreas de los picos de 4-metilo-3-heptanona y de 2-heptanona en cromatogramas de cabezas de obreras medianas de *A. cephalotes*.

A : Mean and standard deviation

Colony	Ratio of peak-area	
A	18.2 ± 1.6	a
B	11.8 ± 2.0	b
C	8.6 ± 2.2	c
D	6.6 ± 1.7	c

a, b, and c indicate means which are different ($p < 0.05$) by Hartley's test.

B : ANOVA

Source of variability	Sum of squares	Degrees of freedom	Mean squares	F
Treatments	278.0	3	92.7	23.0 ***
Error	52.3	13	4.0	
Total	330.4	16		

*** indicate $p < 0.001$

DISCUSSION

From these experiments we may conclude that *A. cephalotes* workers recognise ants of their species by chemical cues spread on the cuticle which probably originate in the head. Colony-specific recognition seems to be achieved by perception of cephalic volatile substances, but it seems that ants react to these only if the intruder shows movement. That is, dead nestmates are not distinguished from those of other colonies of the same species. It is also possible that the way the volatiles are released from the head is different in an anaesthetised ant or an isolated head from a live ant or a live ant with the legs and gaster removed. There could be different rates of release of the alarm pheromone from the mandibular glands. The biological assays and the chemical analysis of the alarm pheromones from workers of different *A. cephalotes* colonies suggest that the ants use the alarm pheromone complex for recognising their nestmates or alien ants. Major differences in the alarm pheromone such as exist between *A. cephalotes* and *Acromyrmex octospinosus*, can thus be detected easily, even in trace amounts of the pheromone on the cuticle, whereas minor inter-colony differences can presumably be detected by the workers only if sufficient pheromone is released. The alarm pheromones of different species of leaf-cutting ants vary in their components (see Crew and Blum, 1972 ; Riley et al., 1974b ; Parry and Morgan, 1979 ; Blum and Hermann, 1978). The alarm pheromone of *A. cephalotes* and *Acromyrmex octospinosus* differ in that *A. cephalotes* has 4-methyl-3-heptanone as the major component and smaller amounts of 3-octanone, 3-octanol, 4-methyl-3-heptanol and 2-heptanone (Riley et al., 1974b), whereas *Acromyrmex octospinosus* has 3-octanone and 3-octanol as major components (Crew and Blum, 1972).

Inter-colony differences in the alarm pheromone have been reported in other ant species (Cavill and Hintenberger, 1960 ; Bradshaw et al., 1979). *Oecophylla longinoda*, for example, shows differences in the composition of cephalic chemicals between colonies of the same species and between castes and ages of workers in the same colony (Bradshaw et al., 1979). Thus, the use of the alarm pheromone as colony-specific recognition signal or even caste-specific recognition signal could be common in ants. Bradshaw (unpublished observations) showed with high speed films that the recognition signal for the detection of *A. cephalotes* ants by *Acromyrmex octospinosus* colonies was mainly the cephalic volatiles of *A. cephalotes*. Thus, at least in leaf-cutting ants, species- and colony-specific individual recognition seems to be achieved using the alarm pheromone.

Ants marking their territory have their mandibles open (Jaffé et al., 1979) which could suggest that they mark their territory not only with the valves gland secretion, but also with their alarm pheromone, which could be used for colony specific territorial marking. Experiments to investigate this possibility require that the relative proportions of the different components must be accurately formulated if synthetic chemical are used.

NEST HYGIENE

Materials and methods

The laboratory colonies of *A. cephalotes* and *Acromyrmex octospinosus* were used for this study. Fifty observations on individual ants of different *Acromyrmex octospinosus* colonies and twenty on *A. cephalotes* workers were carried out. In each observation, an object (piece of spent fungus, freshly-cut leaf, dry leaf, etc.) was placed on a specific area of the nest (food place, waste dumping place or nest), and the activity displayed and the route walked by the ant which picked up the object, were recorded on a scale map of the corresponding nest table. The time spent in each activity was noted separately. Each colony had a different distribution of nest area on the tables. Despite this, the following areas could be clearly identified in each colony : nest, food place, waste dumping place (waste pile), and the trail leading to the food place. All observations were performed in day-time between 11:00 am and 2:00 pm (lights off at 4:00 pm). Experiments in the dark were performed using red safety lights.

Results

The waste dumped by the ant colonies in the laboratory cultures consisted mainly of spent fungus and dead nestmates. Occasionally, pieces of paper or other materials used in experiments were found in the rubbish pile. The dumping place was generally on the nearest edge of the table from the nest. When the nest was shifted in position on the table, ants began to dump their waste materials at a site, parallel in position from the former one. This suggests that the ants do not use marks or permanent chemical trails to find the position of the waste dumping place, but they probably find it by orientating from the nest with the help of general spatial cues.

If a pile of spent fungus is laid on the nest table next to the nest, some ants will begin to dump more waste materials on it. At the same time, other ants will carry the waste from this artificial pile to the one normally in use. Sometimes an equilibrium is established, which allows the artificial pile to exist for various weeks. If the spent fungus is spread over a larger area around the nest, the waste will be transported to the nest and then to the dumping place, without being reinforced with more waste. This suggests that the waste products of the nest, if present in a certain quantity and concentration, will stimulate workers to identify it as a dumping place and therefore use it as such. A piece of spent fungus placed inside the nest, or very close to it, is picked up by workers and carried directly to the dumping place. If a similar piece of spent fungus is placed on a different part of the nest table, it will be picked up in the same way, but is will be taken to the nest. Once in the nest or near the nest entrance, the ant carrying the waste will dump it there and another worker will then take it to the dumping place. Even if the piece of spent fungus is placed near the dumping place, it will be carried to the nest. The ant picking it up in this position, normally comes from having dumped its piece of rubbish and is on the way back to the nest. Only on very few occasions (4 %), could an ant be seen carrying a piece of spent fungus, picked up at a distance from the nest, directly to the edge of the table or to the dumping place. If a dry leaf, or a filter paper impregnated with the defence secretion is placed distant from the nest on the table, it is carried directly to the edge and dumped there. This is true for both ant species studied.

Table VI – Mean time and standard deviation (s) taken by an *Acromyrmex octospinosus* worker carrying a freshly-cut leaf (F) or a piece of spent fungus (R), from either the food site (FP) or the rubbish dumping site (RP) to the nest.

Tabla VI – Media y desviación estandard del tiempo (s) que tarda una obrera de *Acromyrmex octospinosus* en cargar hacia el nido un pedazo de hoja recien cortada (F) o un pedazo de hongo muerto (R), desde la fuente de alimento (FP) o del área del basurero de la colonia (RP).

	FP	RP
F	31 ± 12 (n =11) a	72 ± 42 (n =8) b
R	156 ± 98 (n =18) c	24 ± 12 (n =11) a

a, b, and c indicate the means which differ significantly ($p < 0.05$) using the Student's t-test.

Table VII – Mean time and standard deviation (s) taken by an *Acromyrmex octospinosus* worker in carrying a piece of spent fungus (R) or a freshly-cut leaf (F) from the food site to the nest.

Tabla VII – Media y desviación estandard del tiempo (s) que tarda una obrera de *Acromyrmex octospinosus* en cargar un pedazo de hongo muerto (R) o una hoja recien cortada (F) del sitio del alimento al nido de día o de noche.

	Day-time (n =12)	Dark, with red lights (n =9)	Probability (t-test)
R	150 ± 114	162 ± 48	>0.3
F	29 ± 10	56 ± 20	<0.01

A piece of spent fungus, placed near the food source, is carried to the nest over a longer time period than a piece of freshly-cut leaf (Table VI). The inverse is true on or next to the dumping site ; a piece of spent fungus is carried to the nest much faster than a piece of freshly-cut leaf. This slowness to reach the nest does not seem to be caused by a deficiency in orientational cues. If the lights are turned off, and red safe light is used instead, no differences in the time taken to transport the piece of spent fungus to the nest can be observed (Table VII), although an ant transporting a freshly-cut leaf will take a longer time before fingind the trail to return to the nest. If the increased time taken by the ant in finding the nest after picking up the spent fungus on the food place is due to difficulties in orientation (lack of a «rubbish trail» for example), the absence of visual cues should increase it even more, as it does in leaf transport behaviour. Thus, the probable reason for the increased time taken to arrive at the nest and for the tortuous route taken by an ant after finding an «unexpected object» (Fig. 3) is not part of the orientation mechanism.

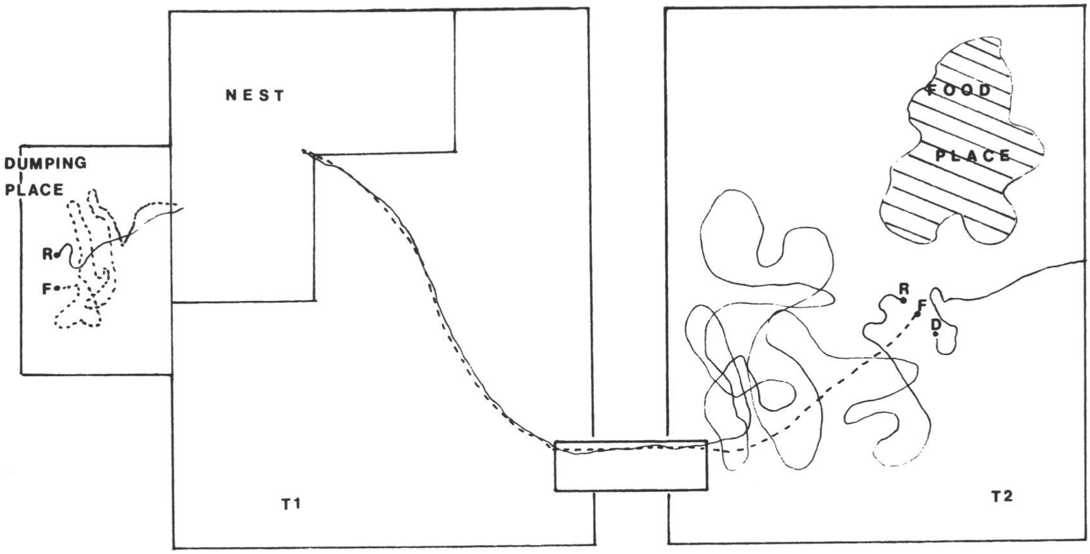

Fig. 3 – Routes taken by *Acromyrmex octospinosus* workers after picking up a piece of spent fungus (R), a freshly-cut leaf (F), or a dry leaf (D).

Fig. 3 – Rutas tomadas por obreras de *Acromyrmex octospinosus* después de recoger un pedazo de hongo muerto (R), una hoja recien cortada (F), o una hoja seca (D).

Solvent extracts of spent fungus, if applied to filter papers, will elicit the same behavioural patterns as a piece of spent fungus. Water is the best solvent, followed by methanol, ether and cyclohexane respectively (Table VIII). All the results have been confirmed in both ant species studied (*A. cephalotes* and *Acromyrmex octospinosus*). Both species have a similar behaviour in regard to nest hygiène. No differences between them could be observed. No species- or colony-specific recognition of the waste products seem to exist in either *A. cephalotes, A. sexdens* or *Acromyrmex octospinosus*. Wastes from the nest are treated in the same way, independently of the colony they originated from.

Discussion

The ability of the ants to find the waste dumping site seems to be based on learning of the route from the nest, although a waste pile in itself may be used as a signal for identification of the waste dumping site of the colony.

Table VIII – Mean time with standard deviation (s) taken by *Atta cephalotes* workers picking up a filter paper impregnated with spent fungus extracts in different solvents. The papers dropped at the rubbish dumping site is indicated in brackets as a percentage of the total number of papers of the same kind presented to the colony.

Tabla VIII – Media y desviación estandard del tiempo (s) que tarda una obrera de *Atta cephalotes* en recoger un papel de filtro, impregnado con extractos de hongo muerto usando diferentes solventes. El porcentaje de los papeles botados en el basurero esta indicado en parentesis en función del total de papeles del mismo tipo ensayados.

A –

Solvent	(n for mean)	Filter paper with extract		Filter paper with pure solvent	
None (Spent fungus)	10	42 ± 55	(100 %)	–	
Water	6	71 ± 61 a	(100 %)	> 1500 c	(6 %)
Ethanol	5	180 ± 112 ab	(100 %)	> 1500 c	(10 %)
Methylene chloride	6	250 ± 198 ab	(100 %)	> 1500 c	(20 %)
Cyclohexane	5	484 ± 244 b	(80 %)	> 1500 c	(30 %)

a, b, and c indicate statistically different means ($p < 0.05$) using Student's t-test.

B – ANOVA for solvent extracts

Source of variation	Sum of squares	Degrees of freedom	Mean squares	F
Treatments	299 462.8	3	99 820.9	3 480 *
Error	516 251.2	18	28 680.6	
Total	815 714.0	21		

* : $p < 0.05$

The fact that a piece of spent fungus, if found in an unexpected place, will induce the ant to transport it to the nest, even if it is found near the dumping site, suggests that an object is first recognized as belonging to the nest and then as a waste product. This suggests that it is the context of the nest which classifies an object as waste or otherwise. The different treatment received by the spent fungus, according to whether it is found in- or outside the nest, does not seem to be related to caste-differences, as can be deduced from the fact that even ants which have just transported waste to the dumping site will behave in the same way as ants which were carrying leaves just beforehand.

The increased length of time taken in transporting a familiar object (spent fungus or freshly-cut leaf) to the nest if found in the «wrong» place suggests a coordination mechanism in the behaviour of ants, which is programmed for certain tasks in specific situations. If an unfamiliar or contradictory situation is encountered, the ant needs time to switch from one activity programme to the other.

The experiments show clearly the existence of two different types of rubbish in an ant colony. One type is the waste from the nest (spent fungus mainly) and the other is probably related to the cleaning of trunk trails (Dry leaves, etc.). These two types of rejected materials are treated differently. One is first transported to the nest, whereas the other is disposed of, without being first transported to the nest. The first type of rejected material is dumped in a specific place, whereas the second type is dumped off the table in any place.

The signal used for recognition of the waste from the nest appears to be chemical, as can be deduced from the experiments using spent fungus extract. Pure solvents on filter papers are not treated as spent fungus, but in a similar way to dry leaves.

These findings suggest that ants treat their waste products from the nest in a careful and special way. A specific programme of behaviour exists, which prevents potentially hazardous materials, capable of breeding diseases which could affect the fungus or the ants, from being disposed of in a random way.

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LEAF-CUTTING ANTS (ATTA SP.), DAMAGE TO AND DISTRIBUTION ALONG BRAZILIAN ROADS

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SUMMARY

Studies were conducted with the objectives of determining the number and probable damage from the colonies of «saúvas» in the zones adjacent to Brazilian highways. Two regions were investigated : the first was a highly populated area of Minas Gerais ; the second was located in an area of low population in untouched woodlands of Pará. In the first area the average number of nests per km was 63.3 and they belonged to *Atta sexdens rubropilosa, A. laevigata* and *A. bisphaerica*. In the second region, the average number of nests per km was 17.3 (the species of *Atta* were not determined).

Reference was made to the fact that *Atta* spp. follow mankind in the «ways of colonization». Also mentioned is their «potential» for soil removal from the subsurface layers in the highway margins. Finally, systematic control of these ants along highways is recommended.

RESUMEN

Las hormigas defoliadoras (Atta sp.), el daño que causan a las carreteras brasileras y la distribución que tienen a lo largo de ellas

Varios estudios fueron realizados con el objetivo de determinar el número y los daños posibles de las colonias de Sauvas en las zonas que bordean las grandes carreteras brasileñas. Dos regiones fueron investigadas : la primera es un área altamente poblada en el estado de Minas Gerais ; la segunda está localizada en un área poco poblada de las selvas intactas en el estado de Pará. En el primer área el promedio de nido por km fué de 63.3, perteneciendo a *Atta sexdens rubrapilosa, A. laevigata* y *A. bisphaerica*. En la segunda región, el promedio de nidos por km fué de 17.3 (las especies de *Atta* no fueron determinadas).

Las especies de *Atta* siguen al ser humano en sus caminos de colonización. También se menciona su potential para remover el suelo de la superficie a los lados de las carreteras principales. Finalmente se recomienda un control sistemático de esas hormigas a lo largo de las carreteras principales.

INTRODUCTION

Of the 14 species of leaf-cutting ants which exist in the American continent, 9 are found in Brazil and one of these has 3 sub-species. These fungus-eating ants are widespread in the whole territory. Their damage to crops is well-krown in Brazil and abroad. Wilson (1971) cites the «sauvas» as the «Kings of Brazil» and Brazil as a «big nest of ants».

Considering the different species of these ants and the great losses from them to crops and native vegetation they can be considered as the «major pest of Brazilian agriculture».

The species of «sauvas» were studied by Autuori (1941, 1942a, 1942b, 1947, 1949, 1950e, 1956a, 1956b) and Gonçalves (1945, 1951, 1960), among others. Literature on the losses to man made constructions due to these ants is scarce. Only Nogueira (1975) tried to quantify such losses.

MATERIAL AND METHODS

Areas along two Brazilian highways were tested : the first was located in a well urbanized area in the state of Minas Gerais and the second was in an area of extremely low population in the State of Para. In Minas Gerais the area tested was on Highway BR 120 between the cities of Viçosa and Ponte Nova, involving 46 km. In Para, the tests were conducted on the Transamazônica Highway, between Altamira and Itaituba : the length of the area was 45 km.

On the first highway one km out of every 5 km was surveyed completely and the ant nests were counted, regardless of their size, on each side of the road, between the road and the limiting fences. Two zones were recognized : road cuts (close to the road shoulders) and from the road shoulders to the fences.

The nests of the three ant species which occur in the Viçosa region were counted : *Atta sexdens rubropilosa* («sauva limao») *Atta laevigata* («sauva cabeça de vidro») and *Atta bisphaerica* («sauva mata-pasto»). The survey was made in the period September 4-10, 1974.

The same procedure was used in the second area, i.e, a survey was made every 5 km. One kilometer along the road for 5 m on each side of the road due to the difficulties of deeper penetration because plant regeneration along the Transamazônica is spectacular. In the counts of the number of ant nests the size of their areas were considered, as shown in Table I. This survey was made on October 17, 1975.

Table I – Nest classification of *Atta* spp by area (obtained by multiplying their greatest length by their greatest width).

Tabla I – Classificación de los nidos de *Atta* spp por área.

Classification	Size of the area
Small	smaller than 15 m^2
Medium	from 15 to 25 m^2
Big	greater than 25 m^2

RESULTS AND DISCUSSION

First region :

The result for this region are presented on Table 2.

Table II – Nest number of *Atta sexdens rubropilosa, Atta laevigata* and *Atta bisphaerica* per km, of road shoulders. Data from 7 observations along the BR - 120 highway (Viçosa - Ponte Nova), Minas Gerais, Brasil.

Tabla II – Número de nidos de *Atta sexdens rubropilosa, Atta laevigata* y *Atta bisphaerica* por km de borde de carretera. Datos de 7 observaciones a la largo de la carretera BR - 120 (Viçosa - Ponte Nova), Minas Gerais, Brasil.

	Number of nests / 3 species		
Km	Road shoulder	Right of way	Total / km
10	55	4	59
15	66	14	80
20	66	24	90
25	57	13	70
30	35	13	48
35	31	17	48
40	35	13	48
Total / area	345	98	

Variance analysis of total numbers in the two zones showed highly significant differences between them. In terms of percentage, it means 77.9 % of the nests were along the highway margins and 22.1 % away from the edge of the road.

During their normal growth these ant nests can cause severe damage to the paved roads. This damage is produced by the removal of soil below the surface by the ants. The damage is in the form of lowering and crunching of the roads which facilitates water penetration. That the soil removal can be of great potential is evident if we consider that the general average is 63.3 nests/km and of these 19.28/km occur very close to the margins of the roads.

According to Autuori (1947) 22.720 m^3 of loose soil was removed from a nest 6 years and 3 months of age. The loose soil that was occasionally carried away by wind or rainfall was not taken into account. It can be readily observed that in the 46 kilometers between the cities and, considering only the road shoulder, there is a «potential» soil removal of 46.000 m^3. This figure could become higher if it is considered that the life of a «sauva» nest can be over 14 years, as observed by Autuori (1947) in a similar study.

Second region :

Table III – Nest number of *Atta* spp/km classified in 3 sizes, within 5 m of road shoulders. Data from 9 observations. Transamazônica Highway, Altamira - Itaituba, Para, Brazil.

Tabla III – Número de nidos de *Atta* sp./km, clasificados entre 3 tamaños dentro de una franja de 5m al borde de la carretera. Datos desde 9 observaciones. Transamazôna, Altamira Itaituba, Para, Brasil.

Km	Number of nests/Classification/Area Big 25 m^2	Medium 15 à 25 m^2	Small 15 m^2	Total/Km
4-5	5	5	70	80
9-10	2	2	60	64
14-15	0	0	0	0
19-20	2	0	20	22
24-25	0	0	5	5
29-30	0	0	0	0
34-35	0	1	1	2
39-40	0	0	0	0
44-45	0	0	0	0
Total	9	8	156	173

The great majority of nests are of small size. The probable reason for this is the age of the road ; the Transamazônica highway had been completed for less than 3 years at the time of the survey. It is also observed that there are 2 peaks of nest concentration : kilometers 4 and 19. Such concentrations can always be seen in areas close to human concentrations.

In the first 10 km of the road, colonization, forest cutting and farms already existed. At km 19 the first school was created ; therefore man is present there.

The tendency of ants to follow man has already been mentioned by some authors. Gonçalves (1970) mentions it for *Atta sexdens* in Forest areas of Parana. He goes on to say that «the species was invading the areas following the trail of colonization». In the present study the presence of a few colonies of «sauvas» in places far from human concentrations, along open roads, in virgin forests, where the number of natural enemies is very high was verified. This low number of ant colonies was observed even 3 years after opening of the highway. The aim next year is to make another survey in order to follow the charges in size and number of colonies during the last 5 years period .

CONCLUSION

The existence of a very great «potential» for the soil removal from the subsurface layers next to highway margins by the «sauva» ants (*Atta* sp.) is verified. This is due to the normal growth of colonies along the highways. In the first region studied the average number of colonies was 63.28/km while in the second the figure was 17.33/km, this being a recently opened road.

The «sauva» nests should be considered as a biological hazard to the Brazilian highways and should be taken into account in the building of new roads. Systematic control on the roads already existing is recommended.

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DIVERSIDAD DE ESPECIES DE HORMIGAS CORTADORAS Y TERMITAS DE TUMULO EN CUANTO A LA SUCESION VEGETAL EN PRADERAS PARAGUAYAS

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RESUMEN

Comunidades de plantas, termitas y hormigas cortadoras fuerón estudiadas en praderas en Paraguay. Las diversidades de especies de hormigas cortadoras demostrarón una associación negativa a las diversidades de especies de termitas. Las cosechadoras de pastos se relacionarón con una baja diversidad de especies de pastos, y un patrón similar se demostró entre las cosechadoras de plantas de hoja ancha y la diversidad de especies de plantas de hoja ancha. Estos patrones sugieren que las hormigas cortadoras, y posiblemente las termitas, favorecen una diversidad inferior de plantas de su recurso alimentício principal. Mediante los análisis de componentes principales y factores comunes, las relaciones entre las diversidades de especies de hormigas cortadoras, termitas y plantas sugierõn que ellas podrían influir a los suelos, y consecuentemente la sucesión vegetal. La regulación de poblaciones de *Atta capiguara* por modos dependientes de la densidad sugiere que la competencía entre especies puede establecer las comunidades. Además, existió una associación altamente negativa entre las diversidades de especies de termitas y de hormigas cortadoras, la cual sugiere que hay competencía entre ambas. Se plantea la posibilidad de que las termitas y hormigas cortadoras, mediante complementación entre las cofradías de cosechadoras, pueden mantener comunidades vegetales en condiciones de desclimax, sobre todo en habitats saturados con colonias de estos insectos sociales.

SUMMARY

Species diversity in leaf-cutting ants and mound-building termites relationed to vegetal succession in Paraguayan grasslands.

Species diversities of leaf-cutting ants and mound-building termites were studied along successional strata in Pleistocene Paraguayan grasslands. Termites and leaf-cutting ants are implicated in altering the soil dynamics of the successional strata through principal component and factor analytic examinations. This effect may be produced directly, through their constructions, or indirectly, through their preferential harvesting of plant species. Strong negative associations were found between termite and leaf-cutting ant diversities, suggesting competition between these two groups. The diversities of the major vegetative resource, either grasses or dicots, was inversely related to the species of ants or termites that exploited them. For grass-harvesting species, for example, these were associated with a low grass species diversity. This suggests that preferential harvesting may maintain a low species diversity of their major food type. Evidence is given for density-dependent colony age structuring in *Atta capiguara*, strongly implying the role of competition in stabilizing communities. Through guild structuring, entailing specializations on vegetative resources, it is hypothesized that a balanced grass and forb species diversity can be maintained. It is also hypothesized that a disturbed habitat can be maintained at a disclimax due to the effects of preferential harvesting within guilds, and to the concomitant changes in the soil mineral dynamics influenced by termites and leaf-cutting ants.

Las hormigas cortadoras (*Atta* y *Acromyrmex*) y las termitas de túmulo son elementos muy caracteristicos de la fauna de las zonas subtropicales surenas de Sud América. Pese a ser la plaga principal de la agricultura neotropical (Cramer, 1967), desconocemos la ecología y el comportamiento de la mayor parte de las especies. En cuanto a las termitas de túmulo, encontramos un patrón similar (Araujo, 1970). Al contrario a las termitas, las hormigas cortadoras alcanzan una riqueza de especies mas elevada en los subtropicos sureños que en los trópicos. Hasta 7 especies de hormigas cortadoras pueden coexistir en comunidades estructuradas (Fowler, 1983), pero al igual que las termitas, llegan a ser elementos dominantes debido a su abundancia y patrones complejos de comportamientos. Aún en comunidades ricas de especies de hormigas cortadoras y termitas, las especies poseen especializaciones de comportamiento y ecología que las permiten coexistir en cofradías (guilds).

Debido a la poca atención que se ha prestado a los insectos sociales del subtrópico neotropical, se ha llegado a formular pocas cuestiones acerca de la ecología de comunidad de los mismos. Aún los patrones básicos de colonización y las relaciones de las especies con los demás elementos bióticos y abióticos no se han examinado. Empero, para las hormigas cortadoras, sabemos que las incidencias de colonias son altamente correlacionados con el grado de la modificación del habitat por el hombre (Eidmann, 1935 ;Fowler, 1983). No obstante, sabemos poco sobre las acciones de las hormigas cortadoras y de las termitas sobre las comunidades vegetales en las cuales viven, con la excepción de la influencia de los nidos sobre la sucesión vegetal localizada (Bucher y Zuccardi, 1967 ;Fowler, 1977 ;Jonkman, 1978 ;Mac Fayden, 1950 ; Glover, Trump y Wateridge, 1964).

Las investigaciones que presentamos a continuación fueron realizadas para examinar la diversidad de especies dentro de comunidades de hormigas cortadoras y termitas de túmulo con respecto a las variables principales de la sucesión. Un análisis más detallado de todos los componentes será presentado en otra parte (Fowler y Haines, 1983). Los estudios se realizarón en el Departamento de Caaguazú, Paraguay, en 1975 y 1976. Se recolectarón datos sobre hormigas cortadoras, termitas de túmulo, plantas y suelos de campos que varían de edad, estimada por el tiempo desde el último disturbio (arado) por el hombre. Estos terrenos fueron propiamente «campos cerrados», los cuales originalmente eran dominados por arbustos, como *Camponesia* (Mirtaceae), hierbas leguminosas y pastos bajos, sobre todo en los campos abierto (Anonimo, 1959). Esta praderas ocuren como islas rodeadas por bosques subtropicales. Estas islas cuentan con una vegetación pleistoncénica muy disimular a la vegetación de derivación más reciente.

PATRONES DE LA SUCESION

Se tomaron muestras de 5 etapas de sucesión, las cuales se llamaran a continuación por su código :

Etapa	Tiempo desde disturbo	historia
a	~ 0.5 años	campo de algodón, en cultivo
b	~ 1.0 años	maizal, dejado al barbecho
c	~ 3.0 años	maizal, plantado con pasto Bermuda
d	~ 10.0 años	soya, abandonado hace 10 años
e	>100.0 años	nunca aprovechado, con arbusto

Los patrones de distribución de hormigas cortadoras, termitas de túmulo, y plantas de hoja ancha y pastos se presentan en las Figuaras 1 a 3. Las termitas (Fig. 1, mano izquierda) y las hormigas cortadoras (Fig. 1, mano derecha) demostraron mayor abundancia en la etapa *d*. Se registraron además

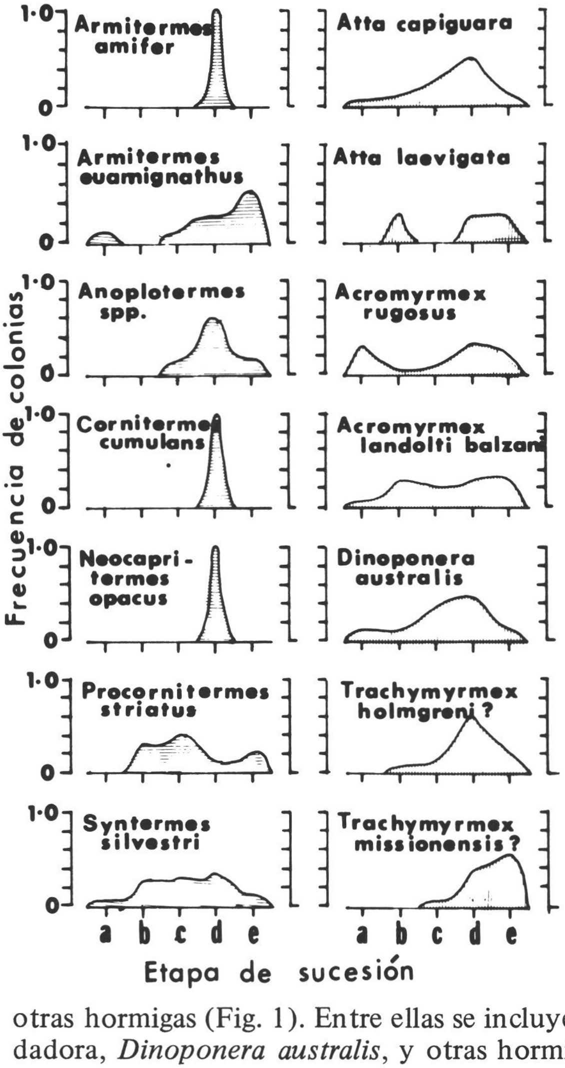

Fig. 1 – La distribución sucesional de hormigas cortadoras y termitas. Los valores representan la contribución proportional del estrato a la representación total de colonias de la especie en todos los estratos.

Fig. 1 – Successional distribution of leaf-cutting ants and termites, given as the percent contribution to the total representation of the species along all successional strata.

otras hormigas (Fig. 1). Entre ellas se incluyeron colonias de la hormiga depredadora, *Dinoponera australis*, y otras hormigas Attini, *Trachymyrmex holmgreni* y *T. missionensis*, las dos registradas por primera vez en el Paraguay. Sin embargo, esta hormigas no formaban elementos de gran importacia, y no están incluidas en los análisis siguientes. Cabe señalar, empero, que la termita *Syntermes silvestri* fué observada frecuentemente cortando el pasto, de modo similar a las hormigas cortadoras. Este comportamiento fué reconocido hace mucho tiempo (Silvestri, 1903), y sugiere que *S. silvestri* quizás se conforma más a las cofradías de hormigas cortadoras de pastos que a las demás especies de termitas.

Las plantas de hoja ancha fueron mejor representadas en la etapa *c* y la etapa *e* (Fig. 2), mientras que los pastos demostraron una abundancia relativa mayor en las etapas *a, d* y *e* (Fig. 3). Estos patrones, resumido en la Figura 4, sugieren que la abundancia de las termitas y de las hormigas cortadoras tiene una relación con una riqueza de más baja especies vegetales, pero con una relacion positiva a la abundancia de las plantas leguminosas.

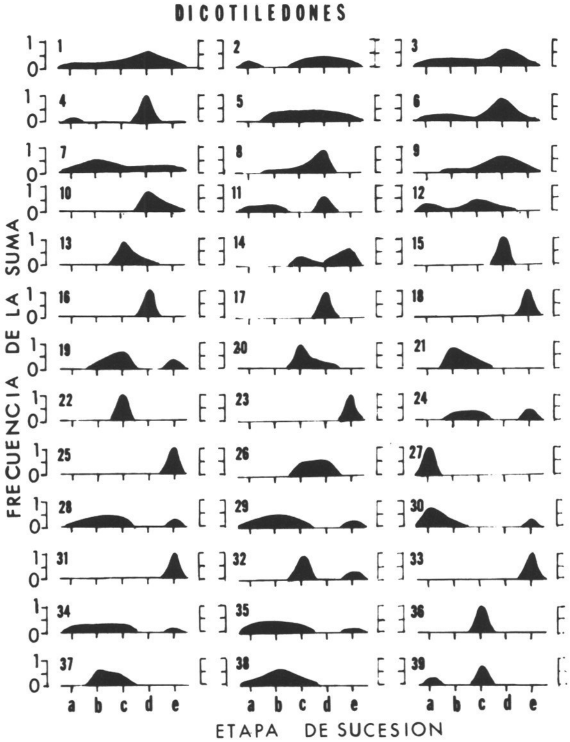

Fig. 2 – La distribución sucesional de plantas de hoja ancha, registrada como en la Fig. 1.

Fig. 2 – Successional distribution patterns of dicots, recorded as in Fig. 1.

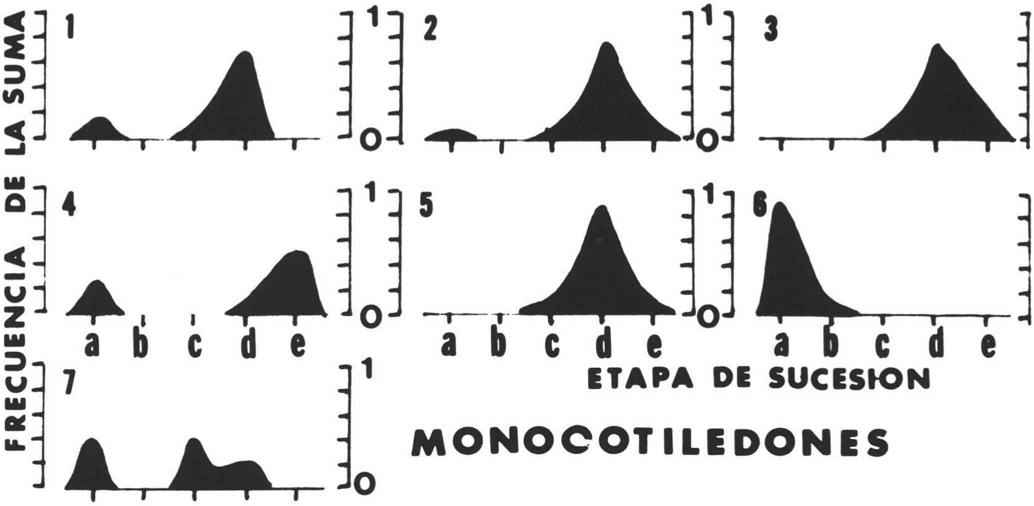

Fig. 3 – La distribución sucesional de pastos, registrada como en la Fig. 1.

Fig. 3 – The successional distribution patterns of grasses, recorded as in Fig. 1.

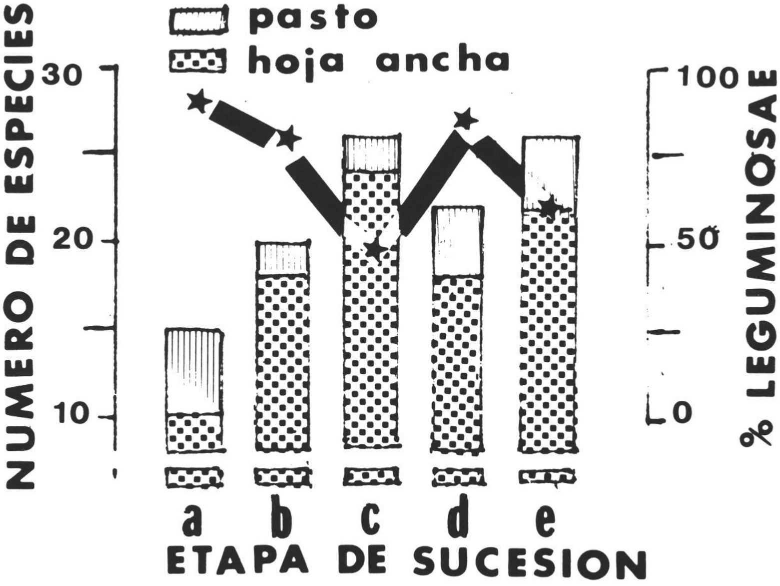

Fig. 4 – La riqueza de especies de pastos y plantas de hoja ancha con respecto al estrato de la sucesion. Los datos para las leguminosas se refieren a la contribución proportional de estas a la suma de todas las plantas individuales de hoja ancha.

Fig. 4 – Dicot and grass species richness as a function of successional strata. Legume data refer to the per-cent contribution of legumes to the total number of individual plants.

Los índices principales característicos de los suelos se presentan en la Tabla I. Es muy evidente una correlación entre la riqueza de especies vegetales y las concentraciones de cationes de minerales presentes (S.I.B.). En el estrato *c*, el pasto Bermuda parece estar devolviendo cationes minerales al suelo, comparado con los niveles presentes en el estrato *b*. Lo que es dificil explicar es la reducida concentración de cationes minerales en el estrado *d*, ya que se esperaba un aumento mientras que prosigue la sucesión. Aquí es posible que las actividades de las termitas y las hormigas cortadoras han producido cambios significativos en lus suelos (Lee y Wood, 1971 ; Bucher y Zuccardi, 1967). Por ejemplo, la capacidad de intercambio de cationes, estimada aqui como la suma de los cationes minerales dividida por esta cantidad más los cationes de hidrógeno, es en realidad dependiente de la estructura física del suelo. Entonces, parece que densidades elevadas de termitas y hormigas cortadoras pueden producir cambios similares a los observados, debido a sus actividades de nidificación. En su turno, los cambios producidos podrían influir las comunidades vegetales. Un análisis más detallado de la sucesión de plantas, termitas y hormigas cortadoras se hallara en Fowler y Haines (1981).

Tabla I – **Indices de la estructura de los suelos en los estratos de sucesión.**

Table I – **Indices of soil structure for the successional strata**

	Valor para el estrato [1]			
Indice	b	c	d	e
Nitrogeno (% de peso seco)	.06	.09	.08	.08
Suma de Intercambio Base[2]	.77	1.09	.74	1.03
Capacidad de Intercambio de Cationes[3]	2.15	2.45	2.89	2.42
% de S.I.B.[4]	36.04	44.40	26.90	43.37

1 datos del estrato *a* no fueron recolectados
2 S.I.B., la suma de Ca, K, Mg y Na
3 C.I.C., que es S.I.B. mas H+
4 % S.I.B., =S.I.B. / C.I.C., o el porcentaje de saturacion de base

ANALISIS DE DIVERSIDAD DE ESPECIES

Generalmente se considera que la diversidad de especies aumenta mientras que prosigue la sucesión (Price, 1975). Sin embargo, si consideramos solamente comunidades taxonómicas (taxocenes), puede haber que se hallen patrones diferentes. Por ejemplo, en cuanto a las hormigas cortadoras, sabemos que son mas abundantes en habitats de estructura de menor complejidad

Tabla II – Matriz de correlaciones entre los volúmenes de colonias y otros parámetros de la sucesión.

Table II – Correlation matrix of colony volumes and other successional parameters.

		2	3	4	5	6	7	8	9	10	11	12	13	14	15	Clave
1	*A. capiguara*	.57	.47	-.31	-.29	-.23	.29	.48	.44	-.31	-.62	.07	.44	-.07	-.06	hormiga
2	*A. landolti*		.18	-.35	.01	.11	.47	.46	.45	.40	-.35	.21	.45	.43	.44	hormiga
3	*A. rugosus*			-.37	-.07	-.32	-.09	-.22	.52	-.27	04	-.25	.52	-.34	-.25	hormiga
4	*A. euamignathus*				.43	.25	-.12	.08	.13	.11	.20	-.42	.16	-.37	.09	termita
5	*A. amifer*					.42	-.01	-.07	.36	.64	.47	-.29	.36	.07	.21	termita
6	*Anoplotermes*						.18	.34	.26	.44	.25	.12	.23	.26	.04	termita
7	*P. striatus*							.64	-.06	.23	-.11	.57	-.04	.63	.48	termita
8	*Syntermes silvestri*								.36	.11	-.50	.24	.36	.22	.41	termita
9	*C. cumulans*									.11	-.26	-.54	.99	-.39	.22	termita
10	Edad (log) del estrato										.42	.19	.11	.65	.50	–
11	Pasto H'											.01	-.26	.20	-.23	–
12	Hoja ancha H'												-.55	.80	-.07	–
13	*A. capiguara* regresada *													-.39	.26	hormiga
14	*A. laevigata* regresada *														.33	hormiga
15	*A. laevigata*															hormiga

* Datos de densidades de colonias grandes extraidas de fotografias aéreas tomadas 10 años antes de las investigaciones.

(Fowler, 1981a), y es posible que un patrón semejante pueda encontrarse para las termitas de túmulo.

La diversidad de especies consta de dos partes : la riqueza de especies, o el número total de especies ; y la igualidad de sus abundancias. Generalmente, la diversidad de especies está estimada por el índice de Shannon-Weaver, que empleamos aquí, pero existe una justificacion suficiente para no usarlo en estudios ecológicos (Southwood, 1975). Sin embargo, emplearemos métodos multivariables para examinar los patrones de diversidad.

Como las colonias de las hormigas cortadoras y termitas crecen a los largo del tiempo, una medida de su tamaño debe indicar mas su importancia que censos de colonias. Empleando los volúmenes de los nidos, examinemos las relaciones entre las especies y algunos índices de la sucesión (Tabla II). El matríz de correlaciones señala unas relaciones marcadas. Por ejemplo, las cortadoras de pasto, *A. capiguara, A. landolti* y *S. silvestri*, tienen una relación negativa con la diversidad de especies de pastos. Este patron puede implicar que las actividades de ellas puede simplificar sus recursos alimenticios . La diversidad de especies de plantas de hoja ancha se correlaciona negativamente con las densidades pasadas de *A. capiguara*, y positivamente con las densidades pasadas de *A. laevigata*, la cual cosecha ambos tipos de plantas. En cuanto a la edad del estrato, algunas especies (*A. laevigata, A. landolti, Anoplotermes* sp., *A. amifer*, y *P. striatus*) tienen una relación positiva, quizás indicando que no son buenas colonizadoras, mientras otras (*A. capiguara* y *A. rugosus*) tienen una relación negativa.

Para examinar los patrones mas profundamente, analicemos los datos con componentes principales (Morrison, 1976), los cuales permiten examinar la covariancia entre los parámetros. Este análisis explicó 87,9 % de la varianza (Fig. 5). El primer componente principal se caracterizo por pesos vectoriales grandes para todas las especies de hormigas cortadoras y termitas, con la excepción de *A. rugosus, Armitermes* spp., *Anoplotermes* sp., y la densidad pasada de hace 10 años (regresado), y con pesos vectoriales negativos para la diversidad de especies de pastos. Este componente parece representar la asociacion de especies de los estratos de sucesión más viejas.

El segundo componente demuestra la distribución contemporanea de *Cornitermes* y *A. rugosus* en terrenos de baja diversidad de especies de plantas de hoja ancha, en las cuales hubo una exclusion prévia de *A. capiguara* o *A. laevigata*. El tercer componente demuestra los estratos más viejos, los cuales están dominados por una diversidad elevada de especies de pastos, y las especies excluidas del primer componente. Este patron puede compararse con los estratos jovenes, con más plantas de hoja ancha (algodón), que *A. capiguara* colonizó. De modo similar podemos interpretar los demás componentes en términos de associación entre especies con (4) o sin (5) la acción adicional de la diversidad vegetal.

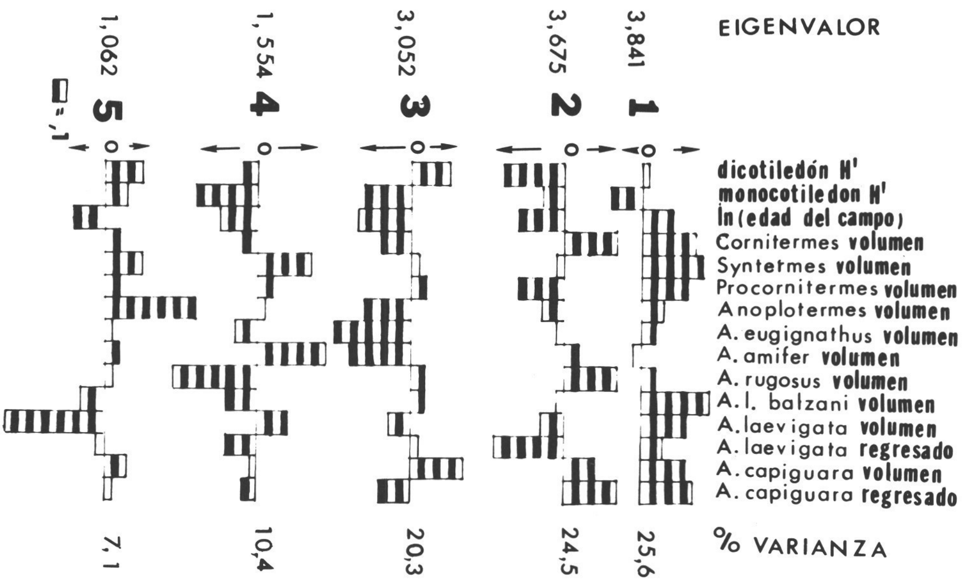

Fig. 5 – Los pesos vectoriales de los primeros 5 componentes principales de matríz de correlaciones de la Tabla III.

Fig. 5 – Variate loadings on the first 5 principal components relating nest volumes and past colony densities (regresado) to the age of the stratum and plant species diversities.

Tabla III – Matríz de correlaciones entre las diversidades de los componentes y los índices de suelos.

Table III – Correlation matrix of component diversities and soil indices.

		2	3	4	5	6	7	8
1	Hormiga cortadora H'	-.60	-.30	.71	-.13	-.32	-.20	-.24
2	Termita H'		.37	-.17	-.04	.63	.38	.29
3	Pasto H'			-.03	.73	-.03	.18	-.08
4	Hoja ancha H'				-.08	-.35	-.08	-.30
5	Edad (log) del estrato					-.37	.51	-.66
6	S.I.B.						.28	.67
7	C.I.C.							-.52
8	% S.I.B.							

Si solamente examinamos la diversidad biótica (Table III) con respecto a los suelos, existen unas correlaciones interesantes. La H' de las hormigas cortadoras tiene relación positiva con la H' de las plantas de hoja ancha, y negativa con la H' de las termitas. Esto sugiere que quizás existe competencia entre las termitas y las hormigas cortadoras ; y que las hormigas cortadoras, las cuales cortan principalmente pastos, favorizaron una diversidad elevada de plantas de hoja ancha. La H' de las termitas tiene une relación positiva con la S.I.B., la cual puede indicar una influencia de las termitas sobre los suelos, o vice-versa.

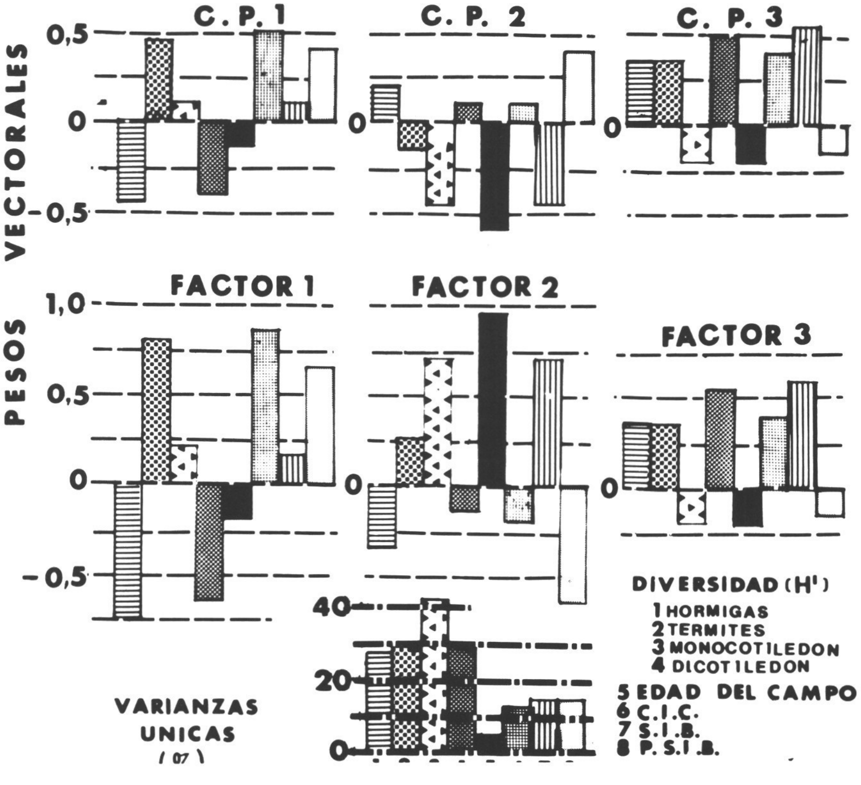

Fig. 6 – Los pesos vectoriales para los primeros 3 componentes principales y los primeros 3 factores comunes, examinando los patrones presentes en la Tabla III.

Fig. 6 – Variate loadings on the first 3 principal components (top) and the first 3 common factors (bottom), relating plant and social insect species diversities to successional time and soil mineral dynamics.

Al sujetar los datos a un análisis de componentes principales (Fig. 6), las relaciones se distinguen mas claramente. En el primer componente principal, lo cual explica 35 % de la varianza, notamos la relación negativa entre termitas y hormigas cortadoras, igual que entre pastos y plantas de hoja ancha. Ya que las hormigas cortadoras cosechaban principalmente pastos y las termitas plantas de hoja ancha, parece que las dos tiendan a simplificar la diversidad de sus recursos alimenticios, lo que favorece la invasión del otro tipo de planta. El segundo componente principal indica la acción de la edad del estrado sobre la diversidad de pastos y S.I.B. El tercer componente principal demuestra la relación entre los suelos (C.I.C. y S.I.B.) y las diversidades de las hormigas, termitas y plantas de hoja ancha.

Imponiendo une relación lineal por medio de un análisis de factores (Fig. 6), podemos extraer un poco más de información. Aunque los patrones observados en los factores comunes y los componentes principales puedan interpretarse de modo igual, podemos deducir como un análisis de factores explica los parametros. Si examinamos las varianzas únicas, vemos que las varianzas únicas para la edad del campo y de los suelos son pequeñas, lo cual implica que podemos interpretar los factores comunes en términos de suelos. Empero, las diversidades de las plaétas y de los insectos sociales no pueden explicarse completemente por los factores comunes.

Si comparamos los resultados de las Figuras 5 y 6, se puede concluir que las especies de hormigas y termitas tuvieron una relación negativa con los pastos o las plantas de hoja ancha, y que esta relación negativa fué dependiente de su principal recurso vegetal. Por ejemplo, si una hormiga cosecha pastos, demuestra una relación negativa con la diversidad de pastos. Es posible que las comunidades de termitas y hormigas cortadoras pueden simplificar la diversidad vegetal, o mantener una baja diversidad vegetal una vez que llenan un habitat. Es también posible mantener una diversidad elevada de especies de plantas para tener cofradías de especies, las cuales podrian rectificar las acciones de las demás cofradias.

Es muy probable que las comunidades de insectos sociales y plantas presentes no existen en equilibrio, sobre todo si la sucesión ocurre, pero pueden demostrar estabilidad ecológica. Si en realidad ocurre un fenómeno tal como descrito, el estrato *d* tendra a existir como un climax de pastos bajos en vez de un matorral de arbustos. ¿Si las comunidades exhiben estabilidad ecológica, como se regulan?

SUCESION Y ESTRUCTURA DE EDADES

Ya que el estrato *d* estuvo saturado, esperaríamos que los controles dependientes de la densidad deben tener un papel importante, más que en los demás estratos no saturados. De hecho, un patrón dependiente de la densidad existe para *A. capiguara* (Fowler, 1983b).

A partir de fotografias aéreas, se halló que las densidades de colonias grandes de *Atta* (hace 10 años) se correlacionaron canonicamente con las densidades contemporaneas de colonias. El patrón observado sugiere que existe una sucesión de especies de hormigas cortadoras en el mismo terreno, la cual depende de la mortalidad de las colonias grandes de *Atta* (Fowler, 1983b).

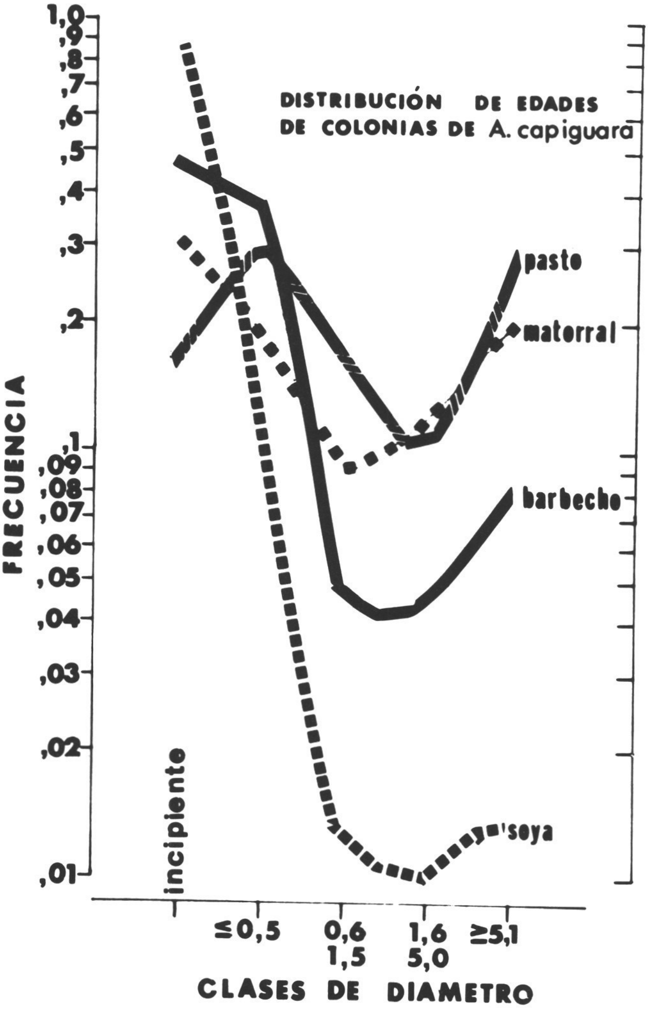

Fig. 7 – Sobrevivencia de colonias de *Atta capiguara* estimada por los tamaños de las colonias presentes en los estratos de sucesión. La sobrevivencia disminuye mientras que la densidad colonial aumenta. Adaptado de Fowler (1983b).

Fig. 7 – Survivorship of colonies of *Atta capiguara* as estimated from colony sizes, and modified from Fowler (1983b). Survivorship decrease as density increases. The strata are : pasto : *c* ;matorral : *e* ; barbecho : *b* ;soya : *d*.

Las distribuciones de edades de las colonias de *A. capiguara* varían de un estrato a otro. La mortandad fué mayor para las colonias pequeñas en el estrado *d*, y despues en *b, e* y *c* respectivamente. Este orden de mortandad o sobrevivencia corresponde a las densidades de colonias presentes, e decir que *d* tenía más colonias y *c* menos. El grado de control de densidades, entonces, depende de la densidad de las colonias presentes, lo cual puede producir comunidades estables.

Para concluir, basándose sobre los datos ya presentados, es muy posible que las hormigas cortadoras y las termitas tengan la potencia de mantener comunidades vegetales en condiciones óptimas debido a la complementación entre cofradias, y la competencia entre miembros de la misma cofradía. Esto permite que varias especies pueden coexistir, y además, las especies de hormigas cortadoras y las termitas posiblemente sirven a determinar los patrones de sucesión vegetal.

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IMPACT OF THE SOCIAL INSECTS ON THE TROPICAL TROPHIC BIOSYSTEMS

FORAGING OF MACROTERMES SPP. (ISOPTERA : MACROTERMITINAE) IN THE TROPICS

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SUMMARY

The Macrotermitinae have a dominant position in most tropical savannas ecosystems.

Macrotermes species, thanks to their symbiosis with a fungus, are able to collect a wide range of plant materials. They have very large nest populations and their energy budget and castes ratios have probably an adaptative value.

On the large territory of each nest, the termite is able to realize both an energy maximization of the food collected (by switching the foraging area throughout the season) and a time minimization (forage being collected in two phases : firstly above ground and stored underground, and secondly conveyed to the nest centre). This foraging territory has a more or less permanent underground structure, leading certainly to a strong influence on the ecosystem : in soil processes and populations control.

The periodic variation of the foraging activity involves day-night cycles and seasonal periodicity. The main foraging takes place in the dry season, for the sexual brood to mature and be ready by the outset of the rainy season.

As far as their reproduction is concerned, *Macrotermes* spp. are «r» strategists. Furthermore, their symbiosis with *Termitomyces* allows them to behave as ultrageneralists : they are then perfectly adapted to fluctuating tropical ecosystems.

RÉSUMÉ

La récolte de nourriture de Macrotermes spp. sous les Tropiques

Grâce à la mise en place de stratégies de récolte particulières, les Macrotermitinae dominent les populations de termites dans la plupart des écosystèmes de savane des zones éthiopienne et indo-malaisienne.

La symbiose avec le champignon (*Termitomyces*) leur permet la récolte d'un large éventail végétal, la digestion de ce matériel et son enrichissement relatif en éléments nutritifs (azote). Leurs colonies très populeuses (10^6 à 3×10^6), où l'énergie est recyclée, peuvent faire face aux périodes rigoureuses en augmentant le nombre d'ouvriers en récolte. Les proportions des différentes castes ainsi que le budget de la récolte ont certainement une valeur adaptative, les différences entre castes de *Macrotermes* devenant plus tranchées lorsque le milieu devient plus fluctuant.

Chez certaines espèces de *Macrotermes*, la récolte s'effectue en deux temps : tout d'abord une collecte à la surface du sol et un stockage souterrain, puis un retour au nid. Ceci permet de minimiser le temps nécessaire pour récolter l'énergie utile (ainsi que l'exposition aux prédateurs). D'autre part, la dimension du territoire de récolte, qui semble plus ou moins constant chez les *Macrotermes* de savane (1100 - 3100 m^2) et le déplacement journalier de la zone récoltée à l'intérieur de ce territoire, maximisent l'énergie recueillie par les termites.

Ce territoire de récolte possède une structure plus ou moins permanente, formée de galeries rayonnantes circulant à 10 - 15 cm sous la surface du sol et débouchant à l'extérieur par des trous de récolte, qui joue certainement un rôle dans la compétition intra- et inter- spécifique.

La comparaison entre les cycles saisonniers de récolte de 4 espèces de *Macrotermes* montre que dans tous les cas, l'activité de récolte maximale se place durant la saison sèche, afin d'assurer la maturation du couvain de sexués qui essaimera durant les pluies.

Le mécanisme régulateur des réserves de meules à champignons est sans nul doute un point essentiel du succès des Macrotermitinae dans les écosystèmes fluctuants tropicaux. En ce qui concerne leur reproduction, cette sous-famille possède une stratégie «r», ce qui, en plus d'un régime ultragénéraliste, leur confère toutes les caractéristiques des espèces colonisatrices.

Recent works indicated the dominant position of the fungus-growing termites in tropical ecosystems, ranging from the Sahel savanna to the Malayan rain forest. The Macrotermitinae represent 37 to 75 % of the total termite live-weight biomass (Josens, 1972, 1974 ; Lepage, 1974a ; Wood & al., 1977 ; Abe, 1979).

The main features of the foraging activities of two *Macrotermes* species have been studied in two semi-arid ecosystems : *M. subhyalinus* Rambur in North Sénégal (Lepage, 1972, 1974a & b) and *M. michaelseni* Sjöstedt in Kenya (Lepage, 1977, 1979, 1981a & b). From the results obtained, it is possible to make some general comments on foraging and feeding within the subfamily Macrotermitinae.

FORAGING STRATEGIES

The Macrotermitinae have evolved several strategies which probably explain their success as evidenced by their high populations and consumption.

Symbiosis with fungus

In all cases, the relative importance of the Macrotermitinae increases when their consumption is taken into account. This is because they have higher weight-specific consumption rates than other Termitidae, as a result of their symbiosis with fungi (Wood, 1978). All aspects of this association have been summarized by Sands (1969). The ecological advantages of growing fungus gardens have recently been pointed out by Cherrett (1980) for the Ants of the subfamily Attini. Broadly, the challenge for the insects is to produce protein-rich tissue from protein-poor food, a hard task for species feeding mainly on litter, like the Macrotermitinae. Table I, established from the data of Matsumoto (1976), shows how the symbiosis with the fungus increases step by step the amount of nitrogen available to the termite :

Table I – Nitrogen content (% of dry weight) and C/N ratio of the food cycling within the nest of *Macrotermes carbonarius* (from Matsumoto, 1976).

Tableau I – Contenu en azote (en % du poids sec) et rapport C/N de la nourriture recyclée à l'intérieur du nid de *Macrotermes carbonarius* (d'après Matsumoto, 1976).

Source	Nitrogen %	C/N
Fragments of leaves stored in the nest	1.3	34.3
Fungus comb	1.7	25.5
Conidiophores	7.3	6.2
Termite major worker	10.0	4.6
Termite major soldier	11.1	4.1

Also, the termite can collect a wide range of plant material although the competitive advantage is not so obvious for termites as for ants, since the former feed mostly on plants at various stages of decomposition (La Fage & Nutting, 1978). Being ultra-generalists is a great advantage in changing tropical systems. Furthermore, the fungus garden acts as an energy pool and buffering mechanism (food supply, temperature, humidity) between the termite colony and its environment.

Nest populations

In savanna ecosystems, the *Macrotermes* mound builders have large populations : mature nests may contain between 10^6 and 3.10^6 individuals (up to 5 1/4 million for *M. michaelseni* in Kenya, Darlington, 1982a). Such high concentration of workers is able to achieve sophisticated homeostatic mechanisms to regulate the temperature and aeration of the nest. The pool of workers is the pathway of a constant recycling of energy. This population has probably evolved under the «principle of stringency», as outlined by Wilson (1975) : the energy budget of the colony is devised to face periods of greatest stringency, where higher numbers of workers are able to search for and to collect food.

Energy budget and castes proportions

As stressed by Wilson (1975), the population structure of social insects has an adaptative value. As far as foraging is concerned, there seem to be at least two main strategies among the species of Termitidae which forage above-ground. They can either forage in the open air, escorted by many soldiers with powerful chemical and/or mechanical weapons, or they can forage mostly under cover in tunnels or galleries or under soil sheeting. That is to say they must use either more anti-predation energy or more building energy. The first strategy is best illustrated by the *Trinervitermes* spp. and the second by most of the Macrotermitinae in arid environments. In the Malayan forest the species which forage under cover have a lower percentage of soldiers (1.2 - 2.8 %) than the ones foraging in the open (17.2 - 29.6 %) (from the data of Abe, 1979 and Abe & Matsumoto, 1979).

Considering the genus *Macrotermes* only, it seems that an decreasing proportion of the energy budget is devoted to soldiers as the environment becomes less humid. Soldiers represented 19.7 % by dry weight of total sterile adults for *M. carbonarius* in West-Malaysia (Matsumoto, 1976 ; 12.7 % for *M. michaelseni* in Kenya (Darlington, 1982a) and only 8.5 % for *M. subhyalinus* in the Sahel (Lepage, 1974a).

Most probably, a better efficiency of the *Macrotermes* colony is due to an optimization of castes rations : the diversification (in numbers and weights) of these castes is well achieved as compared with other Macrotermitinae (i.e. : *Microtermes*). We might expect that differences in sizes and roles between castes in *Macrotermes* species would be less obvious where the tropical environment is less variable (eg forest as compared with savanna). From the few examples available, the weight-ratio between extremes of castes (major soldier versus minor worker) is about 5.0 for *M. carbonarius* in a rain-forest (Matsumoto, 1976), 8.2 for *M. bellicosus* in a southern guinean savanna (Collins, 1977, 1981) and 16.2 for *M. subhyalinus* in a Sahel savanna (Lepage, 1974a). These data agree with Wilson's (1975) statements on ergonomics of castes in social insects.

Territory and foraging behaviour

The foraging behaviour is rather constant in the genus *Macrotermes* (at least in savanna ecosystems) : the foraging populations flow in a network of underground galleries, emerging on the ground surface through foraging holes to collect plant materials back to their nest. Soil shelters, tunnels or trails may be added outside the foraging holes.

The underground network is more or less permanent and defines the territory of the colony, the area where the foraging population collects the available food. Thanks to the possession of such a territory, the termite is able to realize two foraging strategies which are somewhat contradictory for most other insect species :

– Energy maximization (as exposed by Schoener, 1971), which becomes possible on the large territory of a single colony, covering a wide range of habitats, by switching the area foraged every few days and so collecting almost all the food available.

– Time minimization (Schoener, 1971), which consists of minimizing the amount of time required to harvest and secure the available energy. *Macrotermes* workers (especially the majors have large mandibles for carrying large pieces of plant back to the foraging holes and storing them underground. They also come out in great numbers at peaks of foraging activity (cf Nest populations). In that respect, many species of termites forage in two phases. In the first, forage is collected above ground and stored, in the second it is conveyed to the nest centre. An example of this strategy is *Hodotermes mossambicus* (Leuthold, 1973). The same appeared to be true for *Macrotermes michaelseni* in Kenya (Lepage, 1981a, Darlington, 1982a & b). More data being needed to find out if this strategy is also followed in other species of *Macrotermes* where no macerated food materials have been found in nests.

The time minimization behaviour acts also as predation minimization : breaking down of forage into smaller pieces occurs below-ground, where the workers are protected from predators.

THE FORAGING TERRITORY

Structure of the territory

Many authors have noted the undergroung gallery systems of termite colonies (Fuller, 1915 ; Greaves, 1962 ; Ratcliffe & Greaves, 1940), but the detail and extent of the systems have rarely been measured.

A very interesting study by Darlington (1982b) has recently brought much new information about the underground foraging system of *Macrotermes michaelseni* nests in Kenya. A few large radial passages extend outwards at a depth of 50 - 80 cm for up to 10 m from the mound, then rise steeply and level off at 9 - 15 cm below soil level. Here they branch and interconnect to form a network of horizontal passages containing many storage pits. Steep branches lead up to soil surface where they end at foraging holes (which are sealed when not in use). Beyond 30 - 40 m from the mound, the network peters out into blind-ending peripheral passages. Altogether this structure may total about 6 000 m of passages per mound and 72 000 storage pits. Furthermore, Lepage (1977) recorded an average of 22 000 to 50 000 foraging holes per mound. This foraging system has certainly a strong influence in the ecosystem. In the area studied in Kenya, the mounds density reached 4 per ha, or a total of 17 km underground passages, 190 000 storages pits and more than 150 000 foraging holes (Darlington, 1982b and pers. comm. ; Lepage, 1977, 1981a).

Size of the territory

We would expect a positive relationship between the population of the colony and the size of its territory : Banerjee (1975) found a linear relationship between the mound height (proportional to the population) and the size of the colony territory, in *Odontotermes redemani*.

The territory of a mature colony of *Macrotermes* seems rather similar even in different ecosystems : 1 100 m^2 in Sénégal (Lepage, 1974) to 3 100 m^2 in Nigeria (Wood & Ohiagu, 1976). The number of foraging holes per nest is also similar : up to 50 000 in Kenya (Lepage, 1977), 30 to 40 000 in Sénégal (Lepage, 1974a). However, the intensity of foraging in a given area can vary, as is shown for example by the density of foraging holes, 10-15 /m^2 both in Kenya and Nigeria, but higher in the Sahel savanna : 20-60 /m^2.

Periodic variation of the foraging area

In one particular night, the workers forage only in a small part of the territory ; the total area foraged per month in Kenya, for *Macrotermes michaelseni*, was 133 m^2 in February and 600 m^2 in July (Lepage, 1977). This pattern, night after night, achieved a nearly full exploitation of the area.

Territory and competition

Such territories certainly play a key role in regulating the populations, as concluded by Kluijver & Tinbergen (1953) : with a density of 1.9 m of underground passage per m^2, some young nests are probably prevented from establishing themselves. Probably the food supply is the ultimate limiting factor, as stated by Wilson (1975) and argued also by Wynne-Edwards (1962). In this hypothesis, one of the function of territory in *Macrotermes* would be to limit the populations.

Darlington's observations (1982a & b) corroborate this hypothesis : she established that a territory is somewhat «alive» as the old passages of an old mound, 28 m from the nest studied, were incorporated into the passages of the living nest. In other cases, an old nest could be taken over and therefore used as subsidiary chambers for growing fungus-combs.

Lepage (unpublished observations) estimated an intra-specific predation of nearly 10 % on established young field colonies of *M. michaelseni*. Bouillon (1970) reported Mathot (unpublished observations) on a nest of *M. bellicosus* near Kinshasa which was not approched by nests of *Cubitermes sankuriensis* because of the territory of the *Macrotermes* mound. Lepage (unpublished observations) recorded real densities of mounds on 14 plots (1.5 to 3.9 mounds/ha), together with their nearest neighbouring distances and the number of trees (50 to 492/ha). Mounds were overdispersed at all site, probably because of their territoriality but a highly negative relationship was found between the mounds overdispersion (departure from a random distribution) and the number of trees per average nest (which could be a rough estimation of habitat diversity). In other words, in a diversified environment, the mounds tend to be randomly distributed.

PERIODIC VARIATION OF THE FORAGING ACTIVITY

Daily activity

Bouillon (1970) proposed the hypothesis that foraging tends to occur in termites when the outside temperature departs the least from the temperature within the nest. Since the temperature within *Macrotermes* nests is around 28 - 30°C (Ruelle, 1964) this hypothesis is rarely realised, except maybe in Sahel, where *M. subhyalinus* started its activity in the evening at 25°C in January and 32°C in March (Lepage, 1974a), the peak of activity occured between 22 h 30 and 0 h 45 (at 23 to 26°C). In Mokwa (Nigeria), *M. subhyalinus* never started foraging before 21 h (Wood, 1978). It appears that each species of termite reacted to the temperature cycle of its own distribution area : *M. michaelseni* foraged in colder conditions in Kenya than *M. subhyalinus* in Sénégal. Broadly, high temperatures prevent foraging in the evening and low temperatures stop foraging in the early morning.

In the case of *Macrotermes michaelseni*, as stated above, the foraging activity was split into two phases : one above the ground, the more obvious, stronghly affected by temperature and evaporation and probably by predation, and the other under the ground, much more inconspicuous. A special device was used in Kenya to study this underground activity (Lepage, 1977, 1981a) : a single nest was surrounded by a trench and the broken underground galleries were reconnected by clear plastic tubes in which the in- and out-going foraging populations were counted at intervals. The total population outside the nest was determined from the balance between the in- and out-going populations. From the comparison between the populations, above and below the ground, two conclusions can be drawn : first, there is a good relationship between the two foraging populations. At the night peak of foraging, about half of the population never appeared above the ground. But secondly, the underground activity continued before and after, when the above-ground activity had ceased and when the foraging holes were closed. From these comparisons, foraging in two phases has been postulated, as quoted above (Lepage, 1981a), corroborated by the fact that the in-going workers were never seen carrying large pieces of food in their jaws but most smaller fragments. The later discovery of storage pits by Darlington (1982b) supported the hypothesis.

Seasonal periodicity

There are many scattered observations on seasonal variations of foraging activity in the literature (reviewed by Wood, 1978). The seasonal periodicity is more obvious in areas where the climatic conditions are most variable (Bouillon, 1970). Hovewer, a general pattern is sometimes difficult to establish clearly, since activity fluctuates greatly between days. Only continuous observations give the real picture of seasonal activity. This conditions, rarely fulfilled, could explain some of the contradictory conclusions found in the literature.

An explanation of seasonal variation in foraging was sough in climatic factors (mainly temperature and rainfall). Bodot (1967), in studying the foraging activity of *Macrotermes bellicosus*, found a positive relationship with the maximum temperature of the 24 h before, with the mean temperature and with the range of relative humidity ; and a negative relationship (though not significant) with rainfall and the number of rainy days.

Detailed work has been done during 3 years (1976-1978) in Kenya, on foraging activities of *Macrotermes michaelseni* (Lepage, 1979, 1981a & b). The daily activity was monitored over 116 days and was found to be positively related to the maximum temperature of the day before and negatively to the rain of the 5 previous days. The monthly relationship over the 3 years showed that the two factors, temperature and rainfall, could explain 33 % of the foraging activity.

Hovewer, the climatic factors alone could not explain all the foraging activity, especially the periods of intense foraging when internal factors depending on the internal economy of the termite colony are preponderant. Swarming lowered the foraging activity. But the main explanation concerning where the maximum foraging activity took place in all the *Macrotermes* species, is the maturation of the sexual brood within the nest. Foraging is clearly a response to increasing needs of the colony.

From the results obtained in Kenya on *M. michaelseni* (Darlington, 1977, 1982a ; Lepage, 1977, 1979, 1981a & b), there was a relatively good agreement ($P < 0.05$) between the foraging activity on the ground (expressed as the number of foraging holes open) and the food balance of the colony (expressed as the ratio fungus-combs weight versus population biomass).

From the figures given by Bodot (1967), it is possible to establish a negative relationship between the food availability (ratio fungus-combs weight to queen weight) and the intensity of the recent foraging activity (ratio of fresh to old fungus-comb). This could explain the constant adjustement of the foraging to the needs of the colony. As a matter of fact, as quoted by Darlington (pers. comm.), though the total weight of the reproductive brood within the nest of *M. michaelseni* varied widely throughout the year, the quantities of fungus-combs showed less variations than expected : it is postulated a feed-back mechanism which constanly adjust the food collected to the consumption by the population. In the other hand, Darlington (pers. comm.) found good correlations between fungus-combs weight and all population parameters (including queen's weight).

Figure 1 brings together four seasonal foraging cycles of *Macrotermes* spp. in different ecosystems, from the data of Lepage (1974a), Wood & al. (1977), Lepage (1981a) and Bodot (1967). The monthly rainfall and the sexual brood maturation within the nests and the swarming time are plotted

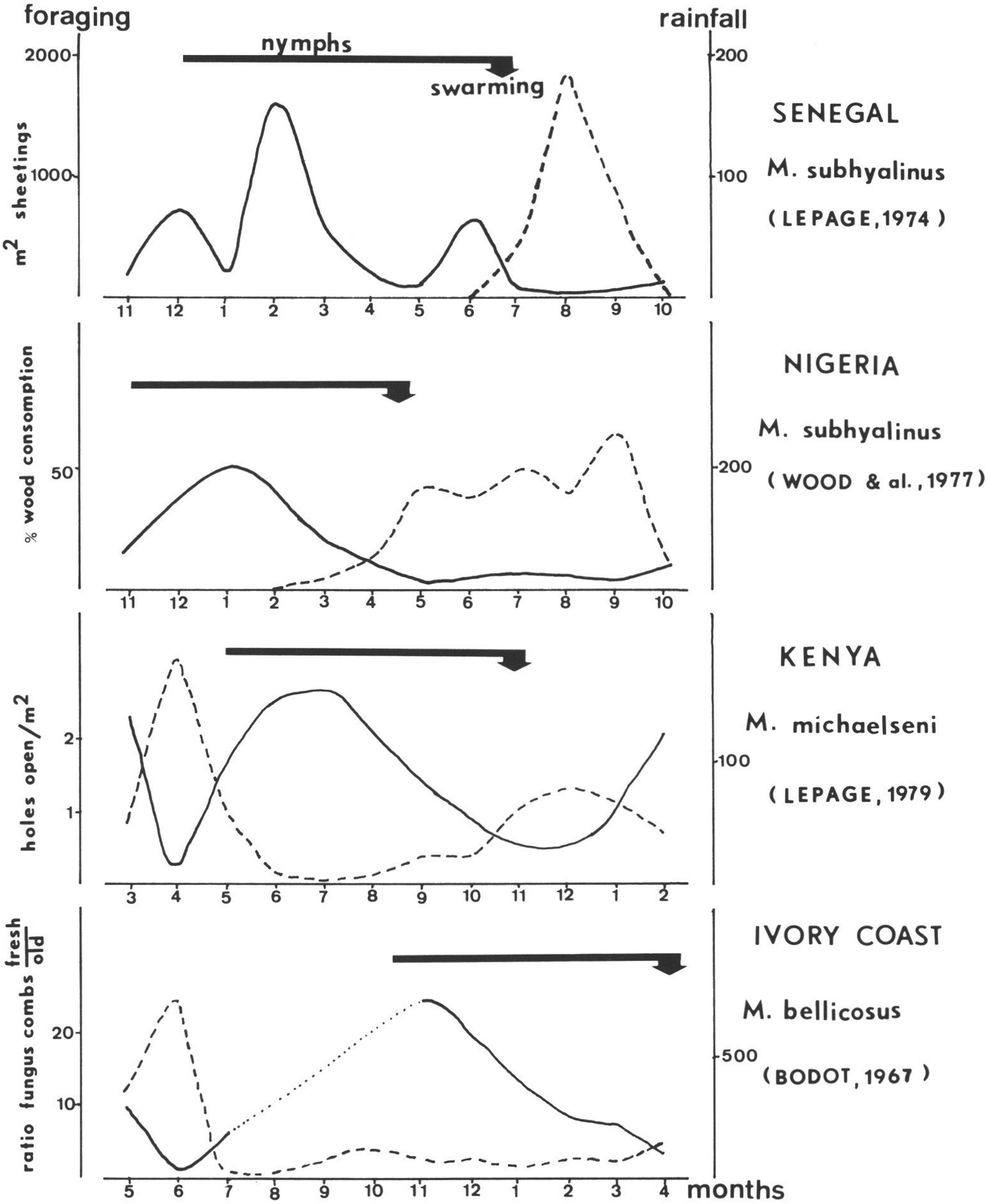

Fig. 1 — *Macrotermes* spp. foraging cycles in four savanna ecosystems (continuous line : foraging cycles ; dashed line : monthly rainfall).

Fig. 1 — Cycles d'approvisionnement de *Macrotermes* spp. dans 4 écosystèmes de savane (ligne continue : cycle d'approvisionnement ; ligne pointillée : précipitations mensuelles).

on the same figure. For all the species studied, the peak of foraging occured during the first third of the nymphs' development, and the maximum food availability within the nest appeared probably one or two months later.

Since the swarming in all the species studied took place at the beginning of the rainy season, the nymphs' development (5 - 7 months) continued through the dry season, and therefore the peak of foraging activity is located in the dry season. The maturation of nymphs during the dry season in seasonal environments is essential for the successful foundation of new colonies in the rainy season.

DISCUSSION

The success of the Macrotermitinae, and especially the *Macrotermes* species in tropical ecosystems, can be partly explained by their foraging strategies. The fungus-combs are probably a buffering mechanism within the termite colony. Besides their role in degrading plant material, the combs are certainly used as food reserves consumed in periods of starvation. Wood & Johnson (1978) showed that in cultivated ecosystems, *Microtermes* spp. rely on combs during the dry season, resulting in a 50 % reduction in total weight of these reserves in 1-year maize, or in an almost total consumption in a 8-years cultivated field. The high energy demand of the sexual brood, particularly important in the Macrotermitinae, can only be met thanks to the combs reserves during the dry season.

Macrotermitinae are «r» strategists, at least as far as their production of sexuals is concerned : these reproductives sometimes represent more than half of the colony biomass. From the few data available, it seems that an increasing proportion of the budget is devoted to reproduction as the environment become more unpredictable.

Being «r» strategists and ultrageneralists, the Macrotermitinae have all the characteristics features of colonial species and are well adapted to new and fluctuating ecosystems of the tropical zone.

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THE EFFECT OF GROUP SIZE ON THE SURVIVAL AND FEEDING ECONOMY OF PSEUDOWORKERS OF BUILDING DAMAGING CRYPTOTERMES SPP. (ISOPTERA, KALOTERMITIDAE)

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SUMMARY

5 replicates of groups of 1, 2, 4, 8, 16 and 32 pseudoworkers of *Cryptotermes brevis, C. dudleyi* and *C. havilandi* were kept on beech (*Fagus sylvatica*) veneer for 60 days. There were no significant species differences in survival. Single individuals survived much less well than groups of 2, and groups of 2 less well than groups of 4 or 8. Production of neotenic reproductives and the establishment of a male-female pair was slower in *havilandi* than in the other two species, but was no less successful. Many groups of 8 or more became potentially successful colonies, and some groups of 4 in *brevis* and *dudleyi*. More neotenics were produced by *brevis* than by the other two species, and differences in survival, neotenic production and establishment of a pair suggested a strain difference between *brevis* from West Africa and from Brasil. Progressive attack on supernumerary neotenics was observed in all three species. Wood consumption was +’ vely correlated with group size in *brevis* and *havilandi*. There was no correlation between wood assimilation efficiency and group size in any species.

RESUMEN

Efecto del tamaño del grupo sobre la supervivencia y la economia de los seudobreros de Cryptotermes **spp. (Isoptera, Kalotermitidae).**

5 repeticiones de grupos de 1, 2, 4, 8, 16 y 32 seudobreros de *Cryptotermes brevis, C. dudleyi* y *C. havilandi* fueron mantenidos en chapa de haya (*Fagus sylvatica*) durante 60 dias. No se manifestaron diferencias importantes de las especies en la supervivencia. Los individuos aislados sobrevivieron con mucha mayor dificultad que los grupos de 2, mientras que los grupos de 2 lo hicieron con más dificultad que los de 4 o los de 8. La producción de reproductores neoténicos y el establecimiento de parejas macho-hembra demostró ser más lenta en la *havilandi* de lo que lo fué en las otras dos especies, pero no por ello menos lograda. Muchos grupos de 8 o de más individuos se transformaron en colonias potencialmente logradas, y algunos grupos de 4 en *brevis* y en *dudleyi*. Un porcentaje mayor de neoténicos fué producido por *brevis* en comparación con los producidos por las otras dos especies. Las diferencias detectadas en la supervivencia, la producción neoténica y el establecimiento de una pareja sugirieron una diferencia de razas entre *brevis* procedente de Africa Occidental y del Brasil. Se observó un ataque progresivo en los neoténicos supernumerarios de las tres especies. La cantidad consumida de madera fué correlacionada de modo positivo con el tamaño de los grupos en la *brevis* y la *havilandi*. No se observó correlación alguna entre la eficacia de absorción de madera y el tamaño de los grupos en ninguna de las especies.

INTRODUCTION

Williams (1977) has shown that colonies of the building pest dry-wood termites *Cryptotermes brevis* and *C. dudleyi* tend to retreat from timber more than about 30 % damaged, and that their numbers decline when the average amount of damage exceeds that figure. One may surmise that at about this point parts of the outer skin of wood remaining are beginning to allow too much gaseous exchange, and may crack, so that the colony finds it increasingly difficult to maintain its water balance and to defend itself against predators. Isolated groups will be increasingly cut off from the main colony as the more vulnerable galleries are abandoned, and in *Cryptotermes* spp., as in other Kalotermitidae, such groups should produce neotenic reproductives readily. It would clearly be advantageous if such groups in building timbers could form small colonies competently, so that the wood was exploited to the full and the maximum number of imagos produced for further colonisation.

The least possible size for such a group would of course be two, a male and a female, but the true least size might be much larger, as it would depend on the ability of the group to maintain itself as a functional colony behaviourally and physiologically. The work of Grassé and his associates (reviewed by Grassé, 1958, and by Harris and Sands, 1965) has shown the importance of the group effect, the mutual sensory stimulation between individuals and, in the lower termites, the trophallactic exchange of food by proctodeal feeding. The purpose of the present work was to determine how small a group might form a functional colony in the three major building pest *Cryptotermes* species found in the western hemisphere.

This study was part of the Centre for Overseas Pest Research (COPR) research programme on building pest dry-wood termites. It was carried out in 1978 by the second author at the COPR termite group laboratory in the British Museum (Natural History), London, as part of a MSc course at London University, his visit to the U.K. being financed by the Consejo Nacional de Ciencia y Tecnologia, Mexico, and the British Council.

MATERIAL AND METHODS

The live material was provided by *Cryptotermes* colonies taken from building timbers or furniture and maintained mainly on beech (*Fagus sylvatica*). The 3 species, with their years of acquisition, were *Cryptotermes brevis* (Walker) from Brasil (1967), Ghana and The Gambia (1973), *C. dudleyi* Banks from Kenya (1976), and *C. havilandi* (Sjöstedt) from Ghana (1973).

Pseudoworkers (wood-feeding instars functioning collectively as a worker caste) were taken from these colonies and randomly made up into groups of 1, 2, 4, 8, 16 and 32 individuals, after the unfit had been removed as described by Williams (1965). Pseudoworkers of at least the 4th instar were used, but brachypterous individuals were excluded as far as possible, and always from groups of fewer than 8, to avoid moults to the pre-imago instar which soon ceases to behave as a pseudoworker. In the event no pre-imagos appeared.

The group sizes were replicated 5 times for each species. The groups within each replicate were matched by being from a single large colony, or else from an amalgamation of 2 or more smaller ones. Colonies of Kalotermitidae can readily be amalgamated, and there was no suggestion in the data subsequently obtained that this practice had any deleterious effect.

Each group was placed on a 40 x 20 x 0.7 mm piece of beech veneer in a 50 x 19 mm glass tube (Fig. 1). The cap of the tube was pierced with a 0,5 mm hole, large enough for gaseous exchange but small enough to prevent internal draughts when handled. The tubes were kept in a container at $28 \pm 1^{\circ}$ and c. 93 % relative humidity for 60 days.

Fig. 1 – A tube set up with 32 pseudoworkers of *Cryptotermes dudleyi*, after 18 days. The two arrowed individuals are a pair of neotenic reproductives.

Fig. 1 – Probeta preparada con 32 seudobreros de *Cryptotermes dudleyi*, después de haber transcurrido 18 días. Los dos individuos marcados con una flecha son una pareja de reproductores neoténicos.

The success of each group was measured firstly by survival, expressed as the mean life length of the individuals in the group. This was obtained from daily counts of survivors, the count being assigned to the mid-point between readings to give the best estimate of true life length ; this applied when counts were missed at week ends and on public holidays. Individuals becoming unfit during the first 3 days were presumed to be handling casualties, and were replaced (3 instances, 1 in each species). At the end of the experiment the surviving individuals were taken to have died on the 61st day for the purpose of analysis.

Besides dead and dying individuals, those which appeared unfit by shortening of the abdomen were also discounted (unless they later recovered), because they had presumably ceased to feed and contribute to the social life of the group. Such individuals often lived for many days before death in the smaller groups, but rarely did so in the larger groups. Their greater vulnerability to cannibalism in the larger groups is suggested by the fact that this mean life length, the social life length, is shorter than that measured by death or a dying condition by only about a day or less in groups initially of 4 to 32 individuals, but by about 3 days in groups of 2 and 12 days in single individuals.

Cannibalism could not be prevented, and so dead and dying individuals were left in the tubes until seen to be infected with mould. They were then removed as it was presumed that no further cannibalism would take place. The work of Dhanarajan (1978) on *Reticulitermes santonensis* suggests that the products of autolytic decomposition would probably make the cadavers repellent before mould appeared.

The second measure of group success was the production of neotenic reproductives, particularly the establishment of a definite male-female pair, after which no further neotenics would be produced, or those which were would live only a short period. This raised the group to the level of a potentially successful colony. Any slight yellowing of the integument or increase in eye pigmentation was noted as the first indication that a pseudoworker had become a neotenic, provided that this was confirmed by further changes. It was found that a female neotenic could sometimes be confirmed to be such by the pink colour of eggs visible through the abdominal wall at a time when other changes were hardly discernable.

The presence of neotenic reproductives stimulates the production of soldiers in *Kalotermes flavicollis* (Springhetti, 1970), a male-female pair having the greatest influence. One 16 group and two 32 groups of *Cryptotermes dudleyi*, and one 32 group of *C. havilandi* each produced a pre-soldier after a pair had been present for 1 to 5 weeks, though in one instance it was not the pair finally established.

Normality of behaviour and physiology in each group was assessed by measurement of the rate at which the wood was consumed and by the efficiency with which the eaten wood was assimilated. The wood consumption of each group was determined as mg oven-dry wood eaten / g termite live weight / day, from the mean number of termites present during the experiment, or the group's survival period if shorter, the mean initial weight of the pseudoworkers of the group, and the oven-dry weight loss of the wood slip. The assimilation efficiency was found as the percentage of eaten wood assimilated by the group, from the oven-dry weight loss of the wood slip and the oven-dry weight of the faecal pellets and other faecal material produced.

No initial oven-dry weight of the wood slips was taken in case the drying affected their food value or moisture holding capacity. Instead, their initial weight was taken after conditioning for 3 days at 45 % relative humidity, fairly close to that of the room in which they were weighed. They were then reconditioned at 93 % RH for at least a day before use. During the experiment any slip as much as 1/3 to 1/2 destroyed was replaced with a second slip, so that many of the 32 groups and some 16 groups had two. At the end the damaged slips were weighed first after reconditionig at 45 % RH, and then after oven-drying to constant weight at 105°. The moisture content of the slip at 45 % RH was then used to calculate an initial oven-dry weight. This should have been sufficiently accurate if there was little variation in moisture content over the slip, or little selection of wood for its moisture content by the termites. The slips were usually attacked in a fairly uniform way by cutting through at various points where the edge of the slip was close to the glass, and by a more general erosion over the surface of the side nearest the glass, the side preferred by the termites for thigmotactics reasons (see Fig. 1). The erosive attack in particular might have allowed selection of the wood, but the slips were chosen for uniformity of appearance and absence of knots, grain irregularities, blue-stain patches and other blemishes, so that any selection should have had a very limited effect.

A problem arose because it was evident, from bizarre values for wood consumption and assimilation efficiency lying far beyond the general level of experimental error, that for reasons unknown some weights of slips and faecal pellets must have been very inaccurate. A small number of grossly outlying values were discarded on the basis of a test for rogue observations (Pearson and Hartley, 1970).

RESULTS AND DISCUSSION

Survival

Table I gives the means of the mean life length values for the 5 pseudo-worker groups of each initial group size. The three species show a broadly similar pattern. Analysis of variance of the whole data indicated no significant species differences, a significant variance ratio for replicates ($F = 2.74$, $P < 0.01$), clearly due to differences within *Cryptotermes brevis* (see below – *Cryptotermes brevis* strains), and a highly significant variance ratio for group sizes ($F = 11.40$, $P < 0.001$). The group size variances are homogeneous by Bartlett's test. The mean life length for single individuals is significantly lower than in groups of 2 ($P < 0.001$), and lower in groups of 2 than in groups of 4 or 8 ($P < 0.05$), by Duncan's multiple range test.

Table I – Mean life length (days), ± S.D., of 5 pseudoworker groups of the initial size indicated in 3 *Cryptotermes* spp. The analysis of overall group means by Duncan's multiple range test is given below. Means sharing the same letter are not significantly different.

Tabla I – Duración media de vida (en días), ± desviación típica, de 5 grupos de seudobreros del tamaño inicial indicados en 3 *Cryptotermes* spp. A continuación se incluye un análisis de los promedios de grupos totales mediante la prueba de alcance múltiple de Duncan. Los promedios que comparten la misma letra no se diferencian de modo importante.

Group initial size	*C. brevis*	*C. dudleyi*	*C. havilandi*	Overall group mean
1	17.9 ± 5.1	28.7 ± 15.9	12.9 ± 4.9	19.8
2	36.6 ± 22.8	45.1 ± 22.1	31.8 ± 22.0	37.8
4	50.3 ± 17.0	48.8 ± 13.0	51.5 ± 10.0	50.2
8	49.2 ± 15.0	54.2 ± 10.6	40.2 ± 6.2	47.9
16	33.8 ± 14.2	53.4 ± 4.0	40.7 ± 7.7	42.6
32	44.9 ± 10.1	51.0 ± 5.8	34.6 ± 13.7	43.5

Group size	1	2	16	32	8	4
Group mean	19.8	37.8	42.6	43.5	47.9	50.2
$P < 0.05$	a	b	bc	bc	c	c
$P < 0.001$	a	b	b	b	b	b

None of the single individuals survived the experiment in a fit condition, only 2 unfit *C. dudleyi* remaining alive. All of the groups of 2 which survived had both individuals living, except in one instance where the first died on the 52nd day. Otherwise no second individual lived long after the first had died. Nevertheless 5 of the 15 groups of 2 survived the test with both fit, so the presence of a second individual considerably enhanced survival. Group of 4 showed the best survival overall, 7 groups surviving with 4 fit individuals, 2 with 3 individuals and 2 with 2 individuals. The results were compressed by the necessity for terminating each replicate at 60 days, the time for the study being limited. But for this the mainly very healthy but sometimes very reduced 16 and 32 groups would certainly have differed significantly from the groups of 2.

It was expected that survival would improve with group size, as Grassé and Chauvin (1942) found in groups of 1 to 10 *Reticulitermes lucifugus* workers. A probable reason for the poorer survival of the 16 and 32 groups, by comparison with the 4 and 8 groups is that any individuals which were rendered slightly unfit by transfer to the experimental conditions, but which

Table II – The mean number of days elapsing before the appearance of the first neotenic reproductive, and before the establishment of a definite male-female pair (number of pseudoworker groups in brackets). The means, ranges and analyses beneath each table are of the 8, 16 and 32 groups only.

Tabla II – El número medio de días transcurridos antes de la aparición del primer reproductor neoténico, y antes del establecimiento de una pareja macho-hembra determinada (el número de grupos de seudobreros se indica entre paréntesis). Las medias, los alcances y análisis incluidos debajo de cada tabla son los de los grupos de 8, 16 y 32 solamente.

First appearance

Group initial size	*C. brevis*	*C. dudleyi*	*C. havilandi*
1	9.5 (2)	8.0 (1)	13.0 (1)
2	16.8 (5)	21.0 (3)	19.7 (3)
4	10.0 (4)	26.3 (3)	11.0 (3)
8	13.0 (5)	7.2 (4)	17.2 (4)
16	6.8 (5)	7.2 (5)	15.4 (5)
32	6.4 (5)	5.8 (5)	16.4 (5)
Mean	8.7	6.7	16.3
Range	4 - 29	4 - 10	6 - 29

Kruskal-Wallis H = 14.68, $P < 0.001$

Mann-Whitney U tests : *brevis - havilandi* $P < 0.01$
dudleyi - havilandi $P < 0.002$

Establishment of pair

2	–	–	–
4	20.7 (3)	49.0 (2)	–
8	20.3 (3)	15.7 (3)	16.3 (3)
16	12.5 (2)	17.4 (5)	29.8 (5)
32	16.0 (4)	11.0 (4)	27.2 (4)
Mean	16.7	14.8	25.6
Range	8 - 32	6 - 31	14 - 40

Kruskal-Wallis H = 9.29, $P < 0.01$

Mann-Whitney U tests : *brevis - havilandi* $P < 0.05$
dudleyi - havilandi $P < 0.01$

could recover, were more likely to be cannibalised the larger the group and the greater the frequency of contact with other termites. The percentages of individuals with shortened abdomens, but seen to recover, amongst the pseudoworkers of the groups of 1 to 32 individuals were, in order of group size, 13, 7, 3, 4, 2 and 0.2 %.

Production of neotenic reproductives

Survival is only the first, though most fundamental, requirement for colony success. No isolated group can become a successful colony unless it produces a male-female pair of neotenic reproductives. Table II gives the mean number of days elapsing before the first neotenic was observed in those groups which produced them, and before the establishment of a definite male-female pair.

Sometimes the first 2 or more neotenics to appear were of the same sex, and in some instances one or both members of a pair might be replaced before a definite pair was established. Observation supported the view of Grassé and Noirot (1946) and other workers that supernumerary neotenics are often attacked by other individuals. In the larger groups the process of cannibalism was so rapid that it was not possible to determine whether the neotenic was attacked or was cannibalised after it had become unfit for other reasons. In the 4 and 8 groups of all three species the process sometimes took 2 days or more, and it was possible to observe that some neotenics received severe injuries to legs and antennae while still active, and were more fully cannibalised as they became unfit and immobile.

Williams (1973) found that neotenics of *C. havilandi* could feed themselves, and that a pair isolated by the deaths of the pseudoworkers in the colony could survive on its own for a long period. However an isolated group of 2 pseudoworkers may rarely be able to become a successful pair. Apart from the probability of both sexes present being only 50 %, survival is further prejudiced by the reduced readines of neotenics to donate proctodeal food, at least in *C. brevis* (McMahan, 1969). Thus the second neotenic of a pair would be less likely to refaunate after its prior moult than when pseudoworkers are present. Here all 5 groups of 2 which survived the experiment had one neotenic and one pseudoworker, but the appearance of two neotenics in 3 of the *brevis* groups was followed by the death of the pair soon after.

The analyses of the data of Table II were carried out only on the 8, 16 and 32 groups because of the disparate numbers of smaller groups producing neotenics, and because brachypterous pseudoworkers, which might be better able to become neotenics than apterous individuals (Wilkinson, 1962), were excluded from groups of up to 4 (see Materials and Methods). The distributions tend to be skewed, as can be seen from the means and ranges, so the Kruskal-Wallis test has been used to compare species (there being no suggestion of significant group size differences). The test indicates significant differences both for the first appearance of neotenics and for the establishment of a definite pair. The Mann-Whitney U tests between species indicate that *C. havilandi* was significantly slower than the other two species in both instances. This is not associated with relative lack of success and may be a characteristic of the species, the reason for which may become apparent when more is known of the long-term development of colonies of all three species, and the natural ecology of *C. brevis* and *C. dudleyi*, whose natural distributions remain unknown.

Colony success

All groups of 4 to 32 individuals producing an established male-female pair (Table II) were healthy at the end of the experiment, except for one *brevis* 4 group which had later died out, and a *havilandi* 32 group the male of which died shortly before the end of the experiment. All the rest, 11 groups each of *C. brevis* and *C. havilandi* and 14 of *C. dudleyi*, out of a possible total of 20 in each species, could be regarded as potentially successful colonies. Thus as few as 4 isolated pseudoworkers might form a successful colony, certainly in *brevis* and *dudleyi* and probably also in *havilandi*, as Wilkinson (1962) noted that a pair might be established by as few as 5 individuals.

4 colonies of *C. brevis*, 5 of *C. dudleyi* and 6 of *C. havilandi* produced eggs, but the open conditions in the tubes precluded the normal handling of eggs by the termites. The greatest number seen was 4, 7 and 3 in the three species respectively, but egg mortality might have been high in some instances. No eggs were observed in the 4 group colonies, but one was seen in a fit but unsuccessful *havilandi* 4 group with a ♀ neotenic.

Cryptotermes brevis **strains**

3 replicates of *C. brevis* were set up with material from Brasil, 1 replicate with material from Ghana and 1 with material from The Gambia, all being adequately comparable as regards the instars represented and the numbers of stock colonies drawn upon. However, examination of the figures for the numbers of neotenic reproductives produced, for survival and for the establishment of groups as potentially successful colonies suggests that the West African and Brasilian *brevis* material may represent two strains with genetically determined differences.

In earlier work (Williams, 1977) it was found that *C. dudleyi* and *C. havilandi* tended to produce a neotenic pair competently, with few supernumerary neotenics, while groups of *C. brevis* produced numerous supernumerary neotenics with a correspondingly high mortality, in the seemingly incompetent pattern found by Nagin (1970) in *Neotermes jouteli*. All the *brevis* material for that study came from The Gambia, and was maintained on balsa in plates of the pattern described by Williams (1973). The mean percentage of individuals observed to become neotenics in the present study in shown in Table III, and the same pattern is shown as before. Regarding species differences, Friedman's $\chi^2 = 9.08$ ($P < 0.01$), clearly due mainly to the consistently much higher percentages in *C. brevis.*

Table III – The mean percentage of individuals observed to become neotenic reproductives in each group size. The numbers of pseudoworker groups are as in Table II. Bracketed figures give percentages for *Cryptotermes brevis* from West Africa (WA) and from Brasil (B).

Tabla III – El porcentaje medio de individuos observados que se transformaron en reproductores neoténicos en cada tamaño de grupo. Los números de los grupos de seudobreros son como los de la tabla II. Las cifras entre paréntesis indican porcentajes para la especie *Cryptotermes brevis* procedente de Africa Occidental (WA) y del Brasil (B).

Group initial size	*C. brevis*	(WA	B)	*C. dudleyi*	*C. havilandi*
1	40	(0	67)	20	20
2	80	(100	67)	20	30
4	40	(25	50)	25	25
8	32	(38	29)	20	27
16	29	(44	19)	16	21
32	18	(22	15)	11	9

The figures for *C. brevis* in Table III are further broken down into means for the 2 W. African groups and for the 3 Brasilian groups of each initial group size. There was a consistently higher proportion of neotenics in the larger W. African groups, and this overproduction of neotenics is associated with very poor survival. Mean life length ± S.D. was 26.9 ± 8.3 days in the 2 W. African replicates, and 46.7 ± 1.6 days in the 3 Brasilian replicates, a significant difference ($t = 3.31$, $P < 0.05$).

The magnitude of the difference suggests that many W. African individuals may have died, or been killed, before their differentiation into neotenics was observable. This has been found in *C. brevis* from N. America by Lenz, McMahan and Williams (in press), though mortality was about as in Australian groups, in which a greater number of clearly differentiating neotenics was observed. However in these strains, and likewise in Hawaii (McMahan, 1963), a pair is usually established, whereas in most W. African groups of 4 or more individuals all the neotenics produced died or were killed, or all but one, or a succession was produced and died without the establishment of a definite pair. Amongst the 20 groups of 4 or more, 9 out of 12 Brasilian groups formed potentially successful colonies, but only 2 out of the 8 W. African groups.

It has been found in experiments of a longer duration than this, that if a *brevis* group successfully establishes a neotenic pair its brood production commonly exceeds that of *dudleyi* or *havilandi* pairs, perhaps because overproduction and cannibalism of neotenics circulates extra protein through the colony (R.C. Steward, personal communication). Thus the W. African strain, if strain it is, may differ from the others mentioned in being poorly adapted to make use of neotenic overproduction.

Feeding economy

Figures for the rate of wood consumption and the efficiency with which the eaten wood was assimilated (Table IV) exclude several gross outliers (see Material and Methods) and two instances where data was accidentally lost. Assimilation efficiency figures could only be obtained where there were enough faecal pellets to weigh with acceptable accuracy, over 0.5 mg, and so were few amongst single individuals and groups of 2.

The amounts of wood eaten by single individuals were so small that their consumption figures were appreciably affected by the experimental error. Hence the -'ve value for *C. havilandi*, the smallest species (mean initial pseudoworker weights : *C. brevis* 4.1 mg, *C. dudleyi* 4,5 mg and *C. havilandi* 2.7 mg), and also the shortest lived (Table I). However the collective figures for the three species, the one assimilation efficiency figure for *dudleyi*, and the fact that all the single individuals produced a number of pellets, albeit usually undersized, indicates that they fed to a slight extent, and perhaps to a level comparable with those in larger groups in some *brevis* and *dudleyi*.

Single individuals of more complex societies suffer a breakdown of normal behaviour and die within a few days, as Grassé and Chauvin (1942) found with *Reticulitermes lucifugus* and the present first author (unpub.) with *Cubitermes testaceus*. However isolated pseudoworkers of *Kalotermes*

Table IV – Mean wood consumption, mg oven-dry wood / g termite live weight / day, and mean assimilation efficiency, % wood assimilated (number of pseudoworker groups in brackets). The species means and standard deviations exclude the figures for single individuals.

Tabla IV – Consumo medio de madera, mg. madera secada al horno / g. peso de termita en vivo / día, y la media de eficacia de absorción, % de madera absorbida (la cifra de grupos de seudobreros entre paréntesis). Las media de las especies y las desviaciones típicas no incluyen las cifras para individuos aislados.

Wood consumption

Group initial size	*C. brevis*	*C. dudleyi*	*C. havilandi*
1	19.3 (2)	12.1 (4)	- 7.1 (3)
2	19.7 (5)	14.5 (4)	13.9 (4)
4	25.1 (4)	15.7 (5)	19.2 (5)
8	23.1 (5)	16.0 (5)	17.6 (5)
16	23.8 (5)	16.2 (5)	24.6 (5)
32	33.5 (5)	18.5 (5)	25.2 (5)
Species mean	25.0	16.2	20.3
S.D.	8.2	10.6	9.01
Assimilation efficiency			
1	–	78.6 (1)	–
2	64.6 (2)	52.4 (3)	79.8 (2)
4	71.1 (4)	59.8 (3)	65.8 (5)
8	70.0 (5)	67.9 (4)	59.3 (5)
16	67.8 (4)	64.5 (4)	63.7 (5)
32	62.5 (5)	65.3 (5)	63.7 (5)
Species mean	67.3	62.8	64.6
S.D.	8.1	10.8	10.4

flavicollis can survive for over a year if artificially refaunated after each moult, the group effect of trophallaxis and stimulation by other forms of contact being manifested by a greater frequency of moulting and caste differentiation (Grassé and Noirot, 1960). Our isolated *Cryptotermes* were able to remain active for several weeks, but feeding was usually reduced and unfitness and death were preceded by a moult in only 4 of the 15 individuals. No part of a shed integument was seen in the tubes of the other 11. So in these species isolation was slowly deleterious, though not catastrophic as in *R. lucifugus* and *C. testaceus.*

The figures for groups of 2 (Table IV) are rather more reliable than those for single individuals. They and the larger groups give mean consumption and assimilation efficiencies broadly similar to values for various Kalotermitidae summarised by Wood (1978).

Groups of 2 to 32 individuals showed a +'ve correlation between wood consumption and the mean size of each group during the experiment, or during its survival period if shorter, in *C. brevis* and *C. havilandi* ($r = 0.62$ and 0.50, $P < 0.002$ and 0.02 respectively). *C. dudleyi* showed the same trend, but not to a significant level. This correlation accords with the expectation that increasing group size and frequency of mutual stimulation would lead to increased activity. However, because of it the figures are not a satisfactory indication of consumption in large colonies kept under similar conditions, which might be appreciably greater than that of the groups of 32 here.

This group effect can be largely removed in an analysis of variance by removing the effect of initial group size differences, the correlation between consumption and initial group size being close to that above. When this is done, the considerable consumption differences between species shown in Table IV are found to be non-significant, as are those for assimilation efficiency.

The expected +'ve correlation between mean group size and assimilation efficiency was not shown by *C. brevis*, and was shown only weakly and non-significantly by *C. dudleyi* and *C. havilandi*, suggesting that the reduced opportunities for trophallaxis in the smaller groups were compensated for by increased pellet eating.

CONCLUSIONS

The most important fact emerging from this work is that very small groups of isolated individuals, as few as 4 pseudoworkers in *Cryptotermes brevis* and *C. dudleyi*, can form a potentially successful colony with an established male-female neotenic pair. Thus it can never be safe to re-use susceptible timber from an infested building if it has had even the lightest penetration by a colony in adjacent wood.

Both survival and the proportion of groups establishing a neotenic pair to become potentially successful colonies was much the same in the three species. However, there were considerable differences in these respects within *C. brevis*, suggesting that the Brasilian and West African material used may represent two distinct strains with genetically determined differences.

Observation confirmed that in all three species some supernumerary neotenic reproductives were attacked while still active and progressively cannibalised, though others may have become unfit for other reasons.

The isolation of single *Cryptotermes* pseudoworkers appeared to have a slow deleterious effect, in contrast to *Kalotermes flavicollis*. Feeding was usually reduced, though it may have been close to normal in a few individuals until they became unfit. Death always occurred within a few weeks, but followed moulting and loss of hind-gut protozoa in only a minority of instances.

Wood consumption in groups of 2 was of the same order as that in larger groups, though their survival was shorter than in groups of 4. Wood consumption rose with group size in *C. brevis* and *C. havilandi*, though not significantly in *C. dudleyi*.

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NITROGEN FIXATION IN NASUTITERMES IN CENTRAL AMAZONIA

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SUMMARY

Twenty one species of termites were collected from their nests in areas of pasture, secondary forest and primary forest at a cattle ranch in Central Amazonia, Brazil. They were tested immediately for nitrogen-fixing (acetylene-reducing) activity. The highest activities (more than 100 nmol C_2H_4 g dry weight^{-1} h^{-1}) all occurred in the genus *Nasutitermes* collected in the pasture. *Nasutitermes* is known to be the commonest genus in the area. Acetylene-reducing activity associated with *Nasutitermes* spp. collected from the same nests on different occasions was very variable, and activity decreased with time after removal of the termites from the nests. Decapitation of the termites stopped activity immediately. The possible role of nitrogen fixation associated with *Nasutitermes* in the nitrogen cycle in Central Amazonia is discussed.

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RESUMEN

Fijación del nitrójeno en Nasutitermes **de Centro Amazonia**

Veinte y una especies de termitas fueron colectadas de sus nidos en áreas de pastos, de selva secundaria y de selva primaria en un rancho de Centro Amazonia, Brasil. Fueron testadas inmediatamente para la actividad de fijación del nitrógeno (reducción del acetileno). Todas las más altas actividades se encontraron en el género *Nasutitermes* colectado en pastos. *Nasutitermes* es el género lo más común en el área. La actividad de reducción del acetileno asociada con *Nasutitermes* sp. colectado del mismo nido en varias ocasiones fué muy variable, decrementando con el tiempo después de remover las termitas de su nido. La decapitación de las termitas paró la actividad inmediatamente. El possible papel de la fijación del nitrógeno asociada con *Nasutitermes* en el ciclo del nitrógeno en Centro Amazonia está discutido.

INTRODUCTION

The regeneration of a tropical rain forest requires a considerable input of nitrogen, part of which may be supplied by biological nitrogen fixation (Nye and Greenland, 1960). Little information is available concerning nitrogen fixation in tropical rain forest. Only since the development of the acetylene reduction technique (Hardy et al., 1968) have such studies been feasible in the tropics. Sylvester-Bradley et al. (1980) found very low rates of acetylene reduction associated with roots of primary forest trees growing on heavy yellow latosol (oxisol) near Manaus, Brazil, even though some of the trees belonged to the family Leguminosae whose members are known for their ability to from nitrogen-fixing root nodules. This lack of nitrogen-fixing activity associated with roots in the rain forest might be due to inhibition of nodulation by the soil, which is acid, low in phosphorus, and has a high aluminium saturation of the cation exchange capacity. An alternative site for nitrogen fixation in the forest might be in the hind guts of termites, which form a large proportion of the soil fauna in Central Amazonia (Fittkau and Klinge, 1973) and which have been shown to possess nitrogen-fixing ability in North America (Benemann, 1973 ; Breznak et al., 1973) and in Australia (French et al., 1976).

Twenty one species of termites were collected from their nests in areas of pasture, primary forest and secondary forest in Central Amazonia. They were tested for nitrogenase activity by the acetylene reduction method. The highest activities (more than 100 nmol C_2H_4 g dry weight^{-1} h^{-1}) all occurred in the genus *Nasutitermes* collected in the pasture (Sylvester-Bradley et al. 1978, Figure 1).

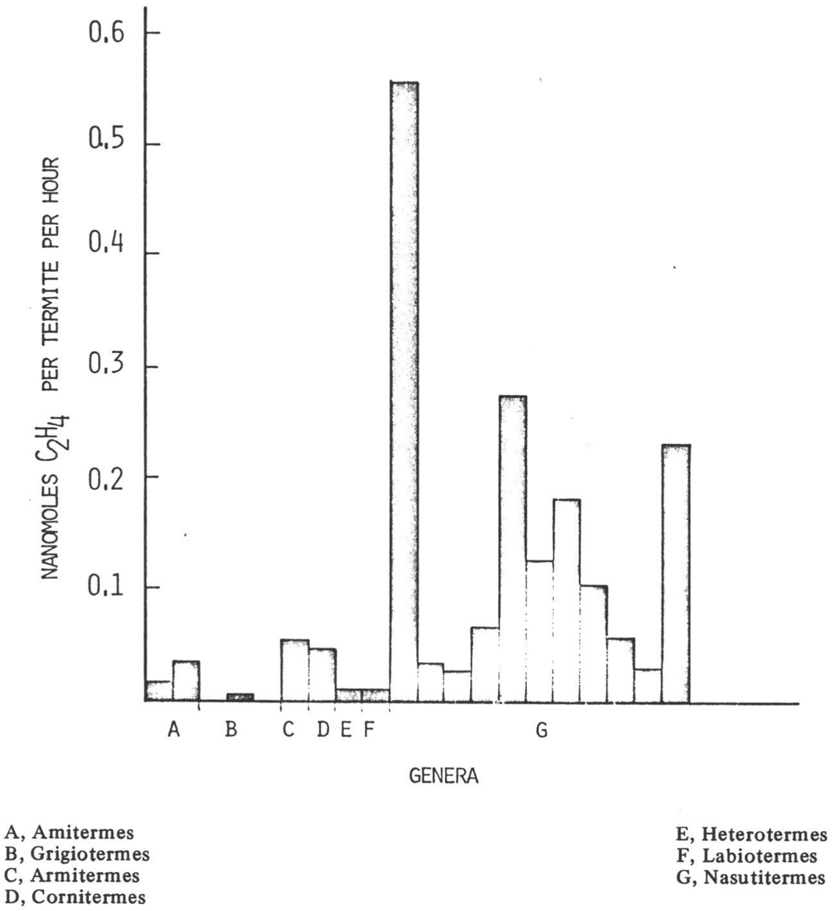

Fig. 1 – Nanomoles C_2H_4 produced by different genera of termites collected in an area of degraded pasture in Central Amazonia. From Sylvester-Bradley et al., *Acta Amazonica 8*, 621-627, 1978.

Fig. 1 – Nanomoles de C_2H_4 producidas por diferentes géneros de termitas colectadas en un área de pastos degradados de Centro Amazonia.

In the experiments described here termites were sampled on several occasions from the same nests in order to obtain more information about their acetylene reducing activity.

MATERIALS AND METHODS

Preliminary experiments were carried out at a farm (Fazenda NAF-6) on the Manaus- Caracarai road (BV-8). For these experiments the nests were broken open and the termites transferred with a paint brush into 7 ml screw-capped bottles. 10 % acetylene was added to the gas phase and after incubation periods of up to five hours gas samples were withdrawn and analysed for ethylene and acetylene on a gas chromatograph with a flame ionization detector as described by Hardy et al. (1968), see figure 2.

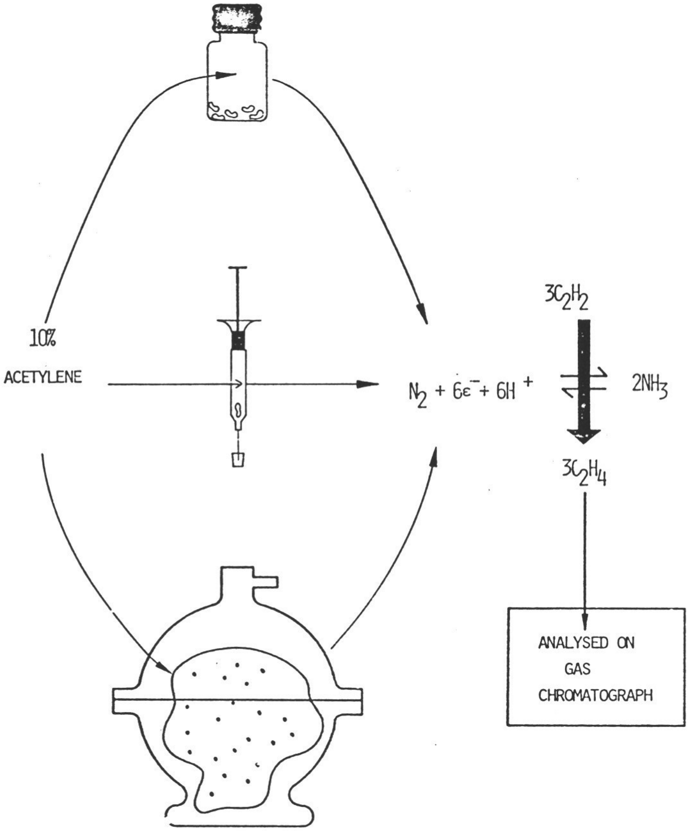

Fig. 2 – Measurement of nitrogen fixation in termites by means of acetylene reduction.

Fig. 2 – Medida de la fijación del nitrógeno en las termitas con el método de la reducción del acetileno.

In further experiments, termites from two nests of *Nasutitermes* spp. on the campus of the Instituto Nacional de Pesquisas da Amazonia (INPA, Manaus) were sampled and tested for acetylene-reducing activity on several occasions by different methods. Large pieces of nest containing termites were placed in desiccators into which 10 % acetylene was injected, individual termites were placed in the barrels of 1 ml disposable syringes, or approximately fifty termites were placed in 7 ml screw-capped bottles as above (figure 2). Acetylene peak heights were used to correct the ethylene peak heights if the containers leaked.

RESULTS

Acetylene-reducing activities of termites collected on two sampling dates from the same nests at Fazenda NAF-6 did not correlate. Termites from one nest showed high activity on the first sampling date and no activity the following week, whereas other nests showed the opposite response (no activity on the first sampling date and high activity on the second). Three large pieces of a nest of *Nasutitermes* sp. containing termites from INPA collected at the same time and incubated in desiccators showed very different activities, and the activity decreased with time (Figure 3).

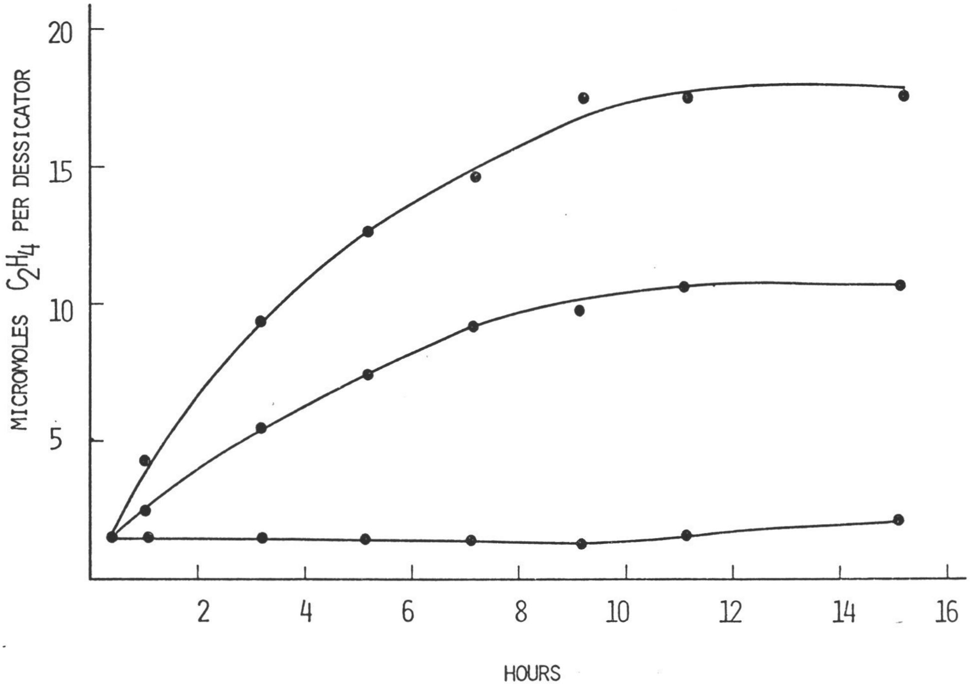

Fig. 3 – Micromoles C_2H_4 produced in desiccators containing *Nasutitermes* sp. within pieces of their nest.

Fig. 3 – Micromolas de C_2H_4 producidas en unos desecadores conteniendo *Nasutitermes* sp. a dentro de pedazos de su nido.

When between thirty and a hundred mixed soldier and worker termites from the same nest of *Nasutitermes* sp. were incubated with acetylene in 7 ml bottles there was no apparent relationship between the number of termites and the amount of acetylene reduced (Figure 4).

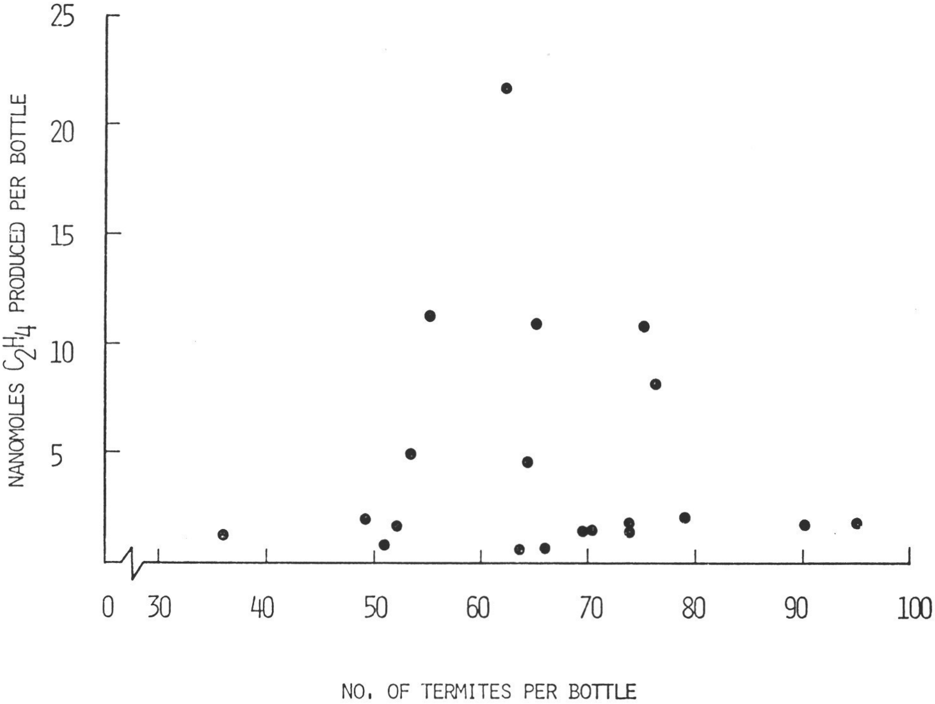

Fig. 4 – Nanomoles C_2H_4 produced in bottles containing between 30 and 100 mixed workers and soldiers of *Nasutitermes* sp.

Fig. 4 – Nanomolas de C_2H_4 producidas en botellas conteniendo entre 30 y 100 obreros y soldados mezclados de *Nasutitermes* sp.

In order to determine wheter this lack of consistency in the results was due to differences between individual termites, single worker or soldier termites of *N. macrocephalus* from a nest in INPA were incubated for five hours with acetylene in the barrels of 1 ml disposable syringes. The soldier termites reduced acetylene whereas the workers did not (Table I). By the end of the experiment the soldiers were still alive whereas the workers were dead.

Table I – Nanomoles C_2H_4 produced by individual *N. macrocephalus* termites incubated in 1 ml. syringes with C_2H_2.

Tabla I – Nanomoles de C_2H_4 producidas por individuos de *N. macrocephalus* incubados en jeringas de 1 ml con C_2H_2.

Soldiers	Workers
0.08	0.00
0.01	0.00
0.11	0.00
0.07	0.00
0.17	0.00

In a further experiment on mixed worker and soldier termites from the same nest of *N. macrocephalus* some of the termites were deliberately killed by decapitation and their acetelyne-reducing activity compared with that of live termites. The live termites reduced acetylene whereas the dead ones did not (Figure 5).

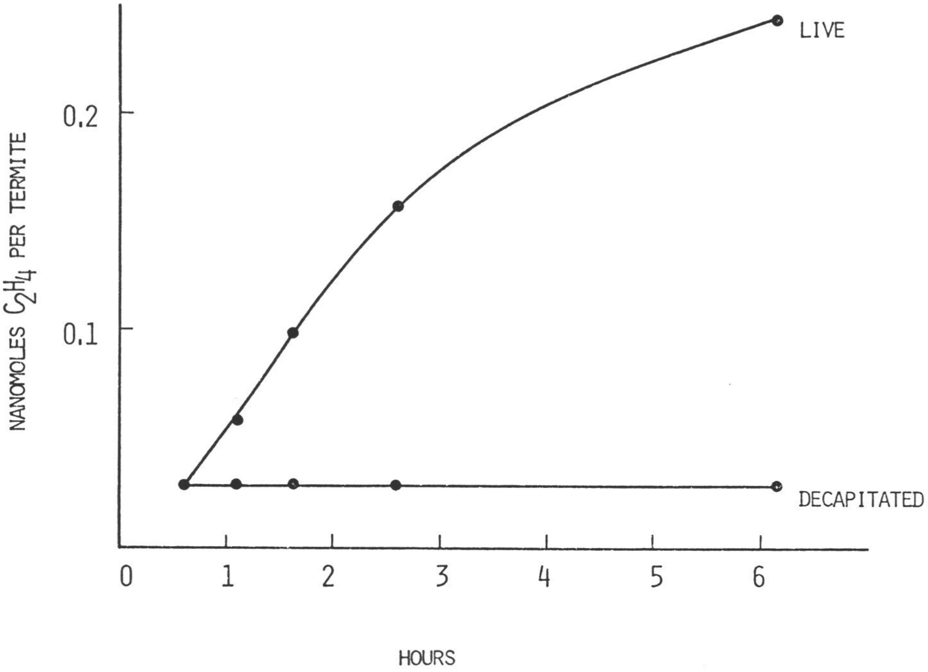

Fig. 5 – Nanomoles C_2H_4 produced by live and dead (decapitated) workers and soldiers of *Nasutitermes macrocephalus* (Mean of 3 replicates).

Fig. 5 – Nanomoles de C_2H_4 producidas por obreros y soldados vivos o muerto (decapitados) de *Nasutitermes macrocephalus* (Promedio de 3 replicados).

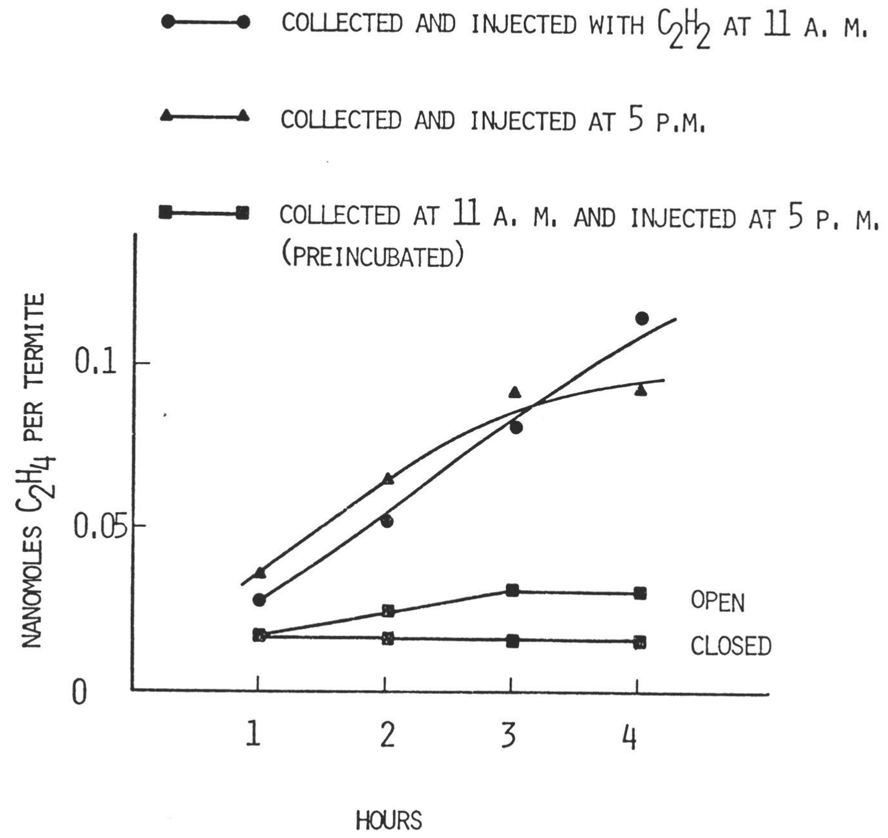

Fig. 6 – Nanomoles C_2H_4 produced by soldier termites of *N. macrocephalus* collected at 11 a. m. or 5 p. m. and exposed to acetylene immediately, or collected at 11 a. and preincubated without acetylene until 5 p. m. Preincubation was carried out either in open or closed bottles.

Fig. 6 – Nanomole de C_2H_4 producidas por soldatos de la termita *N. macrocephalus* colectados a las 11 a.m. o 5 p. m. y expuestos al acetileno immediatamente, o colectados a las 11 a. m. y preincubados sin acetileno hasta las 5 p. m. La preincubación fué llevada a cabo en botellas abiertas o cerradas.

Figure 6 shows that if the acetylene was injected into bottles containing *N. macrocephalus* soldiers immediatly after they were collected from their nest, the activity was higher than if acetylene was injected six hours after removal of the termites from the nest. The activity of termites which had been removed from their nest six hours earlier was slightly higher if the bottles containing the termites were kept open during the six hours than if they were closed.

DISCUSSION

The results presented here suggest that dead termites cannot reduce acetylene, even if tested immediately after their death. This is surprising in that the gut microflora of a termite would not be expected to die immediately on the death of its host. However, it implies that the activity of the termite gut microflora depends very closely on the physiological state of its host and that damage or disturbance of the host may inhibit the microflora's activity. The inconsistent results obtained when sampling the same nest more than once may have been due to changes in the behavior and consequently the physiology of the termites in response to disturbance of the nest.

It is possible that the acetylene reduction method underestimates or misrepresents the nitrogen-fixing activity associated with termites. For example Benemann (1973) and Breznak et al. (1973) reported higher activity associated with worker than soldier termites, whereas here we show the opposite result. This might be due to the worker termites tested by us being more fragile than the soldiers, which caused the inhibition of the acetylene-reducing activity associated with them. Sylvester-Bradley et al. (1978) concluded that the low rates of nitrogen fixation associated with *Nasutitermes* spp. in degraded pasture in Central Amazonia could be limiting the rate of decomposition in this ecosystem, and that the total amount of nitrogen fixed would not be sufficient to supply the needs of a regenerating forest calculated by Nye and Greenland (1960).

In order to draw such conclusions it was necessary to assume a ratio of C_2H_2 reduced to fixed N_2 of 3 : 1, which is not necessarily a valid assumption (Hardy et al., 1973). The results presented here indicate that estimates of nitrogen fixation by termites made with the acetylene reduction technique should be interpreted with great care. The rates of acetylene reduction associated with *Nasutitermes* spp. reported by Sylvester-Bradley et al. (1978) indicate that nitrogen fixation occurs in this genus. However, it is not clear whether the rates were under or overestimated or whether the other genera tested are able to fix nitrogen or not.

In view of the important role played by termites in the decomposition process in tropical ecosystems, the limitation of this process by levels of available nitrogen (Aho et al., 1974), and the lack of an appropriate method for estimating the rate of nitrogen fixation associated with termites, it seems too early to conclude that the contribution of the process to the nitrogen economy of the ecosystem is insignificant.

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FEEDING STRATEGIES OF ANTS IN DIFFERENT WEST AFRICAN SAVANNAS

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SUMMARY

Soil and ground dwelling ant populations have been sampled in two savannas of the Ivory Coast, thus authorizing to compare densities and feeding habits of the ants whilst exploiting the resources of the community. One hundred and twenty species live in the soil. The densities of their nests is about 3500 nests/ha. Soil dwelling Ponerinae shows a highly specialized diet to the expense of several zoological groups (Collembola, Chilopods Geophilidae, ...) Added to these habits their low densities lessen competition and facilitate coexistence. A similar process appears to operate in terrestrial species as the members of *Leptogenys* and *Megaponera* exhibiting a narrow stratification limited to the soil surface. Many ants belonging to the others subfamilies utilize a broad alimentary diet often at the expense of interspecific overlap of the same categories of preys. Speciation seems to play on a broad diversification of activities in space and time which results in an optimal exploitation of the resources. In correlation with a better conservation of the seeds, the percentage of the totally or partially granivorous ants is higher in the drier savannas.

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RÉSUMÉ

Stratégies alimentaires des fourmis de différentes savanes d'Afrique de l'Ouest

Les peuplements de fourmis du sol ont été étudiés dans deux savanes de Côte d'Ivoire. Ceci a permis de mettre en évidence et de comparer entre elles les stratégies de prospection mises en œuvre par les fourmis terricoles et endogées dans l'exploitation des ressources du milieu. Cent vingt espèces de fourmis peuplent les sols. La densité de leurs nids s'élève à environ 3.500 nids/ha. Les Ponerinae endogés s'individualisent d'abord par une spécialisation alimentaire poussée s'exerçant aux dépens de divers groupes zoologiques (Collemboles, Chilopodes géophilomorphes, ...). Ceci, joint à leurs densités souvent faibles, diminue la compétition et facilite leur coexistence. Un processus semblable se déroule chez les fourmis à stratification étroite qui exploitent exclusivement la surface du sol (*Megaponera, Leptogenys*, ...). Les fourmis à stratification étendue subsistent aux dépens de ressources alimentaires variées présentant des analogies entre elles. Elles s'individualisent alors par une séparation marquée de leurs activités dans l'espace et le temps qui conduit à une exploitation optimale des ressources du milieu. Le pourcentage d'espèces totalement ou partiellement granivores s'élève lorsqu'on atteint les zones plus sèche permettant la conservation des graines.

The Ivory Coast is a typical part of West Africa. From the south to the north, this country presents a regular succession of the main geographic area occuring in that part of the black continent. In the South, the dense and compact rain forest extends continuously along the coast of the Atlantic ocean ; more centrally, the humid prairies called «Guinea savannas» sharply replace the rain forest and are covered by a dense and uninterrupted layer of grasses. The annual rainfall varies from between 1100 and 1600 mm according to the year. These open savannas are interspersed with numerous *Borassus* palm trees and in the more central region of the country with *Lophira lanceaolata* trees (Lamotte, 1967). The north is characterised by a sparse vegetation which grows more or less slowly on the lateritic soils. The soil- and ground - dwelling populations of ants were studied between 1963 and 1978 in several savannas of the Ivory Coast ; the main effort taking place in the Lamto reserve (6° 13'N - 5° 02'W). The aim of that study was first to know the composition of the specific spectrum of ants, to measure the densities and the spatial distribution of the nests, and second to determine the magnitude of the populations and their seasonal variations. We then tried to outline the strategies used by different species to coexist when exploiting the resources of the community. These results were compared to those obtained using the same methods in the drier part of the northern savannas.

In the «Guinea savannas», there are two seasons : the dry season from November to April and the rainy season during the rest of the year. Very often the rainfall diminishes in August : this is often called the short dry season. The precambrian substratum consists of granite and amphibolites. The granites, when altered, give ferralitic soils which most often cover hills and plateaux. In the thalwegs, the phreatic water gives birth to hydromorphic soils. All these soils are totally covered by a grass layer made of Graminaceae (*Hyparrhenia* and *Loudetia*) and Cyperaceae interspersed with numerous bushes, small trees (*Crossopteryx, Bridelia, Ficus,...*) and palm tress (*Borassus ethiopum*).

In the «Sudanese savannas», the rainy season extends from June to September. The mean annual rainfall is about 900 mm. Soils are commonly lateritic and grasses become sparse. All these prairies are burnt every year by bush fires which destroy the various grasses more or less completely.

For a satisfying interpretation of the results obtained by the sampling method we must first study the structure of the nests of the commonest species. For this purpose, two methods can be used ; first, digging a circular trench around a localized nest and subsequently opening the structure to describe it, second labelling ant workers with 198 Au mixed with sugar and following that by a detection of the distribution of these workers in the field (Lévieux, 1971). Nest densities were studied by the quadrat method, the quadrats being randomly dispersed in the savanna. In order to localize and collect the cavities where the ants live, 48 quadrats of 16 m^2 each were dug with the aid of 6 workers at – 30 cm during the rainy season (1965) and 48 others during the dry season (1968) –. When located, the place and size of each cavity were positionned on a scale plan of each precise quadrat. In the field, the soil surrounding each cavity from the nest was collected in plastic bags. In the laboratory, the ants were isolated from each earth sample contained in these bags by hand sorting, flottation, Berlese funnels or sifting on the soil. For the larger ant species (*Paltothyreus tarsatus, Megaponera foetens, Leptogenys conradti, ...*) nest densities were estimated just after the annual bush fire by the transect method.

Finally, 120 species of ants living in the soil have been collected. Their average densities are about 3500 nests/ha with significant differences related to the type of soils and the presence or absence of vegetation (burned or unburned savanna) (Lévieux, 1972). Table I shows, for example the quantitative variations of the densities of several common species in two different types of soils. The most abundant ant *Camponotus acvapimensis* has an average density in the ferralitic soils of 400 adult nests/ha with a peak up to

800 nests/ha just after swarming. The lack of suitable space appears to be the major limiting factor for the establishment of new colonies ; consequently the mean density of adult nests remains constant at about 3 to 400 nests/ha. Each adult colony (i. e. more than two years old) consists of about 4000 workers and extends over 20 m^2. The standing crop (dry weight) biomass averages 0.47 g/m^2 in ferralitic soils and 0.20 g/m^2 in hydromorphic soils (Lévieux, 1976). More than 10 other species have mean densities beyond 100 nests/ha and a total standing crop (dry weight) biomasse beyond 1,5 g/m^2.

Table I – Nest densities and percentages from several common ant species ; two types of soils of the guinean savannas are studied here (after Lévieux, 1973, simplified).

Tableau I – Densités de nids et pourcentages de plusieurs fourmis communes ; deux types de sols de savanes guinéennes sont étudiés ici (d'après Lévieux, 1973, simplifié).

Species	Ferralitic soils (total density : 3500 nests/ha)		Hydromorphic soils (total density : 3500 nests/ha)	
	densities/ha	%	densities/ha	%
Camponotus acvapimensis	700	20	320	8
Polyrhachis viscosa	250	7	160	4
Acantholepis canescens	200	5	200	5
Crematogaster sp.	150	4	0	0
Pachycondyla caffraria	120	3	200	12
Hypoponera gr. coeca	160	4	0	0
Pheidole gr. megacephala	160	4	0	0
Pheidole termitophila	120	3	480	12
Tetramorium guineense	120	3	160	4
Mesoponera ambigua	0	0	400	10
Camponotus congolensis	0	0	250	6

The large specific diversity revealed here is interpreted as an example of a maximum utilization of the nutritional resources of the community. Under these conditions, what are the feeding strategies used by ants to coexist when exploiting the resources of the community ? The analysis of the structure of the community deals primarily with the distribution of the nidification site in a vertical space. Several groups of species can be defined :

1 – a group of soil dwelling Ponerinae exclusively nesting in the ground (*Amblyopone, Apomyrma, Mystrium*, ...)

2 – most often terrestrial species digging their nests mainly in the soil (*Paltothyreus, Pachycondyla, Camponotus, Pheidole*, etc.) but sometimes extending it above the ground in dead trunks (*Megaponera, Odontamachus*,...)

3 – the others species of ants living at different places in the vegetation (*Crematogaster*, several *Camponotus*, etc.)

Fundamentally ants use two different and complementary ways to coexist in the ecosystem whilst exploiting the local resources. Soil dwelling Ponerinae hunt simultaneously in relatively narrow zones of vertical space (0 to 1 meter below soil surface) and have very specialized diets (Chilopods for *Amblyopone*, etc., see Table II). This, together with the low densities encountered, lessens competition and facilitates coexistence. A similar process appears to operate among terrestrial species such as the members of *Leptogenys* and *Megaponera*, which behave like raiders. In general in savannas, a specialized died seems correlated with a narrow vertical stratification (Lévieux, 1972).

Table II – The staple food of sympatric specialized predators in the Lamto savanna

Tableau II – Alimentation de base de prédateurs sympatriques specialisé dans une savane de Lamto

Species	Staple food
Soil dwelling species :	
Amblyopone pluto	Chilopods : geophilomorphs
Amblyopono mutica	idem
Apomyrma stygia	idem
Plectroctena subterranea	Diplopods, Julidae
Plectroctena lygaria	Eggs of diplopods
Hypoponera gr. coeca	Collembola
Discothyrea oculata	Eggs of arthropods
Centromyrmex sellaris	Termites
Ground dwelling species :	
Leptogenys conradti	Isopods, Oniscoidea
Leptogenys sp.	idem
Megaponera foetens	Termites

Many phylogenetically advanced species, particularly those belonging to the subfamilies Formicinae, Pseudomyrmecinae and Myrmicinae feed on the surface of the soil and in the trees. The analysis of their mode of food-supply was conducted both at the congeneric level and between species belonging to different genera (Table III and IV). These species have a broad alimentary diet, often at the expense of interspecific overlap of the same categories of prey. Their mode of specialisation in hunting is based on the collecting of resources on a restricted surface or volume. Generally competition is avoided by a differentiation in the harvest area in horizontal or vertical space and a diversification of the of hunting period in the 24 hour cycle. As a result of speciation, the differences in trophic behaviour between congeneric species seems to be more important than between species belonging to different genera. For example, *C. acvapimensis* obtains food by collecting sugar from Aleyrodidae living on grasses. At the same time *C. maculatus* collects sugar from Coccidae fixed on roots.

Competition in horizontal space remains active between terrestrial ants of the savanna. This is correlated with the high degree of soil occupation

Table III – Different utilization of the savanna food resources by three species of *Camponotus.*

Tableau III – Utilisation différente des ressources alimentaires de la savane par trois espèces de *Camponotus.*

	acvapimensis	*solon*	*vividus*
A – Food coming from animals			
Chilopods	+		
Arachnida	+		
Larvae of :			
Orthoptera		+	
Lepidoptera	++	+	+
Dictyoptera		+	
Coleoptera	+	+	
Diptera		+	
Homoptera		+	
Hymenoptera (Formicidae)	+	++	+
Adults of :			
Dictyoptera	+		
Isoptera	+++	+	
Zygoptera		++	
Homoptera		++	+
Coleoptera	+		+
Lepidoptera		++	
Hymenoptera		++	
Diptera			+
Psocoptera			+
B – Food coming from animal exudations			
Cicadidae		+	
Jassidae	+		
Membracidae	+		
Psylloidea	+		
Coccoidea		+	+
Aleyrodoidea	++	++	+++
Alphididea	++		
C – Food coming from vegetal sap and unknown origin			
gum of Anacardium			+++
gum of Sterculia			++
sap of trees, plants	+++	++	

by terrestrial colonies. These ants fight to conquer and maintain control of areas hunting. The territories move about with time. In gallery forest, densities are far lower, which appears to reduce aggressive interactions between arboreal species and between fauna living in different strata of the soil and trees. Peaks of diel activity of congeneric species are separated in time and never coincide. A lesser degree of temporal separation occurs among heterogenic species (Lévieux, 1977).

A detailed comparison of the trophic preferences of the ants living in different types of savannas clearly shows that the percentage of specialized carnivors regularly decreases from the humid to the dry tropics. The exclusive granivores (*Messor*,...) play a major role in highly seasonal areas having a long

Table IV – Some examples of food preferences among Ivory Coast savanna ants

Tableau IV – Quelques exemples de préférences alimentaires chez des fourmis de Côte d'Ivoire

Animal food :

Earthworms	*Paltothyreus.*
Arachnida :	
Spiders	*Atopomyrmex, Camponotus, Platythyrea, Tetramorium.*
Myriapoda :	
Diplopoda	*Paltothyreus, Pletroctena, Psalidomyrmex.*
Chilopoda	*Amblyopone, Apomyrma, Camponotus.*
Crustacea :	
Isopoda, Oniscoidea	*Leptogenys.*
Insects :	
Collembola	*Hypoponera.*
Odonata, Zygoptera	*Camponotus.*
Dermaptera	*Paltothyreus.*
. *Dictyoptera :*	
Mantidae	*Camponotus, Platythyrea.*
Orthopteroids	*Camponotus, Platythyrea.*
Isoptera	*Acantholepis, Camponotus, Crematogaster, Megaponera, Paltothyreus, Pheidole, Platythyrea, Polyrhachis, Tetramorium.*
. *Hemiptera :*	
Heteroptera	*Paltothyreus.*
. *Homoptera :*	
Cicadidae	*Camponotus.*
Ricaniidae	*Atopomyrmex, Camponotus, Platythyrea.*
Others	*Acantholepsis, Camponotus, Crematogaster, Polyrhachis.*
. *Lepidoptera :*	
Noctuidae	*Camponotus, Platythyrea.*
Hesperidae	*Camponotus, Platythyrea.*
Pyralidae	*Camponotus, Platythyrea.*
Geometridae	*Camponotus.*
Others	*Paltothyreus.*
. *Coleoptera*	*Acantholepis, Atopomyrmex, Camponotus, Paltothyreus, Platythyrea, Tetramorium.*
. *Diptera*	*Camponotus, Pheidole, Platythyrea, Tetramorium.*
. *Hymenoptera*	*Crematogaster, Camponotus, Paltothyreus, Pheidole, Platythyrea.*

Plant food :

Leaves	*Crematogaster, Platythyrea.*
Seeds	*Atopomyrmex, Pheidole, Platythyrea, Tetramorium.*
Latex	*Atopomyrmex.*
Sap and others	*Atopomyrmex, Crematogaster, Camponotus, Platythyrea.*

dry season which allows for long term storage of seeds. In the Sudanese savanna of Ferkessedougou only 11 (17 %) out of the 63 sympatric species found are strictly carnivorous. In humid habitats some predators (*Pheidole, Tetramorium*) can become granivorous even in rain forests. On the whole, the ecological niches of the savanna ant species whether phylogenetically primitive or advanced, are complementary, and their feeding behavior appears to contribute to the stability of the multi-species community to which they are well adapted.

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