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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