Promotor   : prof.dr. M.F. Mörzer Bruxns, oud hoogleraar in Natuurbehoud en
               Natuurbeheer aan de Landbouwhogeschool
Co-referent: dr. A. van Wijngaarden, stafadviseur Internationaal Natuurbeheer
               (RIN Leersum)

HABITAT PREFERENCES, DIET, FEEDING STRATEGY AND SOCIAL ORGANIZATION OF THE BLACK SPIDER MONKEY (ATELES PANISCUS PANISCUS LINNAEUS 1758) IN SURINAM

M.G.M. van Roosmalen

HABITAT PREFERENCES, DIET, FEEDING STRATEGY AND SOCIAL ORGANIZATION OF THE BLACK SPIDER MONKEY (<u>ATELES</u> <u>PANISCUS</u> <u>PANISCUS</u> LINNAEUS 1758) IN SURINAM

Proefschrift
ter verkrijging van de graad van
doctor in de landbouwwetenschappen,
op gezag van de rector magnificus,
dr.H.C.van der Plas, hoogleraar in de
organische scheikunde,
in het openbaar te verdedigen
op woensdag 26 november 1980
des namiddags om vier uur in de aula
van de Landbouwhogeschool te Wageningen

(Dit proefschrift is tevens verschenen als RIN-rapport 80/13
van het Rijksinstituut voor Natuurbeheer te Leersum)

CURRICULUM VITAE

Marcus Gerardus Maria van Roosmalen werd op 23 juni 1947 geboren te Tilburg en behaalde in 1966 het HBS-B diploma.

Van 1967 tot 1971 studeerde hij Biologie aan de Rijksuniversiteit te Utrecht. Voor het doctoraal examen, behaald in 1974 aan de GU te Amsterdam, werden achtereenvolgens de volgende onderzoeken uitgevoerd: een 9-maands onderzoek naar de ecologie van de Ree t.b.v. het Rijksinstituut voor Natuurbeheer, Arnhem; een 1½ jaar durend onderzoek naar de anatomie en de evolutie van de hand en het handgebruik bij Primaten (incl. de mens); een systematisch onderzoek aan vruchten en zaden van een aantal families die voorkomen in het tropische regenwoud van Suriname.

Na het behalen van het doctoraal examen werd het beschrijvende onderzoek van vruchten en zaden voortgezet, waarbij hij als tijdelijk medewerker bij het Instituut voor Systematische Plantkunde, Utrecht werkzaam was. Begin 1976 werd dit onderzoek afgerond in een boek getiteld 'Surinaams Vruchtenboek', en werd tevens een beurs toegekend door de Stichting voor Wetenschappelijk Onderzoek van de Tropen, teneinde in Suriname een drie-jarige veldstudie te verrichten aan de autecologie van de zwarte slingeraap (Ateles paniscus paniscus). De resultaten van dit onderzoek zijn voor een deel verwerkt in dit proefschrift. De verzamelde gegevens betreffende de synecologie van alle 8 in Suriname voorkomende Primaten zijn reeds gepubliceerd.

Het in dit proefschrift neergelegde onderzoek werd mogelijk gemaakt door financiële steun van de Stichting voor Wetenschappelijk Onderzoek van de Tropen (WOTRO).

STELLINGEN

I

Autecologisch veldonderzoek aan een diersoort moet voorafgaan aan ethologisch veldonderzoek aan die diersoort.

II

Wanneer het begrip 'semi-natural' gebruikt wordt met betrekking tot dieren in gevangenschap, dient het vervangen te worden door 'pseudo-natural'.

III

Het sociale gedrag van primaten in gevangenschap moet niet bestudeerd worden met de pretentie dat het representatief is voor de soort.

IV

Dat het vruchtvlees van door chimpansees en orang-oetans gegeten vruchten, behorend tot diverse soorten Strychnos (familie Loganiaceae), het giftige alkaloid strychnine zou bevatten, is onjuist.

J. van Lawick-Goodall, 1968. Anim. Behav. Monograph. 1:165 - 311: H.D. Rijksen. 1978. Veenman, Wageningen; R.W. Wrangham, 1975. Ph.D.thesis. Cambridge Univ.

V

De kennis van de relaties tussen plant en dier, en meer in het bijzonder die tussen vruchten en verspreiders, én tussen vruchten en zaadpredatoren, is van groot belang voor een beter begrip van de opbouw en samenstelling van het tropische regenwoud.

VI

Rehabilitatie van primaten, zo deze al mogelijk is, dient slechts te geschieden in die gebieden, waar een geschikt biotoop voorhanden is én waar de oorspronkelijke populatie van de soort verdwenen is.

VII

De ontvolking van Suriname is mede verantwoordelijk voor het feit dat het natuurbehoud en -beheer aldaar ten voorbeeld wordt gesteld in de wereld.

SAMENVATTING

Deze dissertatie beschrijft de biotoopkeuze van de Surinaamse slingeraap (Ateles paniscus paniscus) en belicht de complexe invloed die voedselbronnen in tijd en ruimte uitoefenen op het gedrag van een groep slingerapen in een 350 ha groot studiegebied gelegen in het Raleighvallen-Voltzberg Natuurreservaat in Centraal-Suriname, en wel in termen van het soort voedsel, de identiteit van de voedselplant en de fenologie, als ook in termen van kwantiteit, dichtheid en verspreiding van de belangrijkste van deze voedselbronnen. De studie toont het fundamentele belang van rijp fruit als hoofdvoedsel aan voor de fourageerstrategie van de slingeraap en behandelt de implikaties die het dieet heeft voor het sociale gedrag.

Vanuit het oogpunt van natuurbescherming is deze studie van belang door de nadruk die gelegd wordt op de grote kwetsbaarheid van de slingeraap ten aanzien van jacht en biotoopverwoesting, en omdat hierin gedetailleerde informatie verschaft wordt aangaande biotoopkeuze en dieet-eisen. Aan deze informatie bestaat dringend behoefte teneinde op een verantwoordelijke wijze de plaats van de te beschermen gebieden te bepalen èn het potentieel van reeds voorgestelde beschermde gebieden.

1,2,3. Van de 8 in Suriname voorkomende apesoorten is de slingeraap het meest beperkt in biotoopkeuze. In het Voltzberggebied komt de soort vrijwel uitsluitend in hoogbos voor (92.6%). Randzones worden niet frequent bezocht (14.9%), waarschijnlijk omdat deze weinig geschikt voedsel bieden. Slingerapen zijn hoofdzakelijk te vinden in de bovenste delen van de kroonlaag en in emergenten (72.3%), de onderlaag van het bos wordt zelden gebruikt (0.8%) en hun vertikale verspreiding heeft een benedengrens van 12 meter. Slechts 4 van de 7 belangrijkste bostypen, die het Raleighvallen-Voltzberg Natuurreservaat biedt, worden door slingerapen bezocht, nl. hoogbos, hoog rivieroeverbos, bergsavannebos en pinazwampbos.

4. In totaal 207 verschillende plantesoorten verschaften de slingerapen voedsel, waarvan 68.1% bomen waren. De belangrijkste plantenfamilies, die de slingerapen voedsel bieden, zijn Moraceae en Mimosaceae. De zwarte slingeraap, een overwegend vruchteneter, voedde zich met 171 soorten vrucht, 33 soorten bloem en 28 soorten blad, terwijl 96% van het totaal aantal waarnemingen waarbij vruchten gegeten werden rijpe vruchten betrof. Het eten van termieten en rupsen is definitief waargenomen. De gemiddelde jaarlijkse voedselopname betreft 82.9% vruchten, 6.4% bloemen, 7.9% jonge bladeren, 1.7% bast en 1.0% overige items (rottend hout, pseudobulben van orchideeën, luchtwortels, honing en insekten). De maandelijkse variatie in voedselkeuze staat in nauw verband met de fenologie, en wel als volgt: gedurende het eerste deel van de 'grote droge tijd' (Juli - Oktober), een periode die gekarakteriseerd wordt door een laag vruchtenaanbod, vult de slingeraap zijn dieet aan met relatief hoge percentages bloemen en jonge bladeren, terwijl een groot vruchtenaanbod gedurende de 'grote regentijd' (Maart - Juli) gepaard gaat met erg lage percentages bloemen en jonge bladeren in het dieet. Individueel worden de percentages sterk bepaald door het aanbod in relatie tot de ecologische verandering, maar steeds gaat de voorkeur uit naar rijpe vruchten. Jonge zaden spelen in het algemeen een ondergeschikte rol in het dieet, behalve in de maanden Mei en Juni. Door in het midden van de 'grote regentijd' grote hoeveelheden jonge zaden te consumeren, welke veel eiwit en vet bevatten, lijken de apen reserves op te bouwen voor de komende periode van voedselschaarste (Juli - November).

Slingerapen bleken een belangrijke rol te spelen als verspreiders van de zaden van vele plantesoorten, terwijl enige soorten exclusief door slingerapen verspreid schenen te worden. Zaadverspreiding d.m.v. endozoochorie (d.w.z. via het maagdarmkanaal van dieren) vond plaats bij 138 soorten vrucht (93.5% van het totaal aantal waarnemingen waarbij vruchten gegeten werden), het scheiden van vruchtvlees en zaden en het laten vallen van zaden werd vastgesteld bij 10 soorten vrucht (2.7%) en predatie van de zaden bij 23 soorten vrucht (3.7%). Ateles behoort tot de kategorie 'gespecialiseerde' fructivoren, welke (bijna) al de benodigde koolhydraten, vetten en eiwitten aan vruchten ontlenen. Groot-zadige, voedzame vruchten schijnen een co-evolutie te hebben doorgemaakt met 'gespecialiseerde' fructivoren als hun voornaamste verspreiders, en dit heeft geresulteerd in een grotere kwaliteit van verspreiding dan bijv. kan worden gekonstateerd bij klein-zadige, weinig voedzame vruchten, welke verspreid worden door een groot scala van zowel 'opportunistische' als 'gespecialiseerde' vruchtenetende dieren. Dit co-evolutionaire patroon (de hoge voedingswaarde van het eetbare vruchtvlees bij groot-zadige vruchten) is bijv. te zien bij families zoals de Palmae, Burseraceae, Myristicaceae, Sapindaceae, Loganiaceae, Capparaceae, Sapotaceae en Meliaceae, welke allen vruchten produceren die voor slingerapen van belang zijn. Van de 166 eetbare vruchtesoorten, die door de slingerapen in het Voltzberggebied werden geëxploiteerd, is ongeveer 80% voedzaam en groot-zadig. De overige 20% wordt vertegenwoordigd door klein-zadige vruchten met een geringe voedingswaarde (hoofdzakelijk water en koolhydraten bevattend), zoals vele bessen en vijgen, welke slechts incidenteel geëxploiteerd werden op weg van de ene plant met voedzame vruchten naar de ander. Voedselbronnen van klein-zadige, weinig voedzame vruchten bleken vrijwel nooit de richting van de dagelijkse fourageerrouten te beïnvloeden noch werden zij regelmatig bezocht. Op deze kategorie voedselbronnen, die vaak grote, massaal rijpende vruchtoogsten produceert, kunnen de slingerapen zich nauwelijks verlaten. De vruchtseizoenen van de soorten die behoren tot de eerstgenoemde kategorie, evenwel, duren in het algemeen relatief lang vanwege een min of meer asynchrone vruchtrijping per individu èn tussen individuen van dezelfde soort, blijkbaar omdat het kleine aantal 'gespecialiseerde' verspreiders gemakkelijk overbelast kan worden. De konkurrentie tussen de plantesoorten die behoren tot de eerstgenoemde kategorie om de hooggekwalificeerde verspreiding, welke slechts door een klein aantal verspreiders kan worden geleverd, heeft waarschijnlijk een evolutie teweeggebracht naar verlengde en gespreide, maar elkaar breed-overlappende vruchtseizoenen, welke situatie vereist is voor het bestaan van 'gespecialiseerde' fructivoren.

5. Het fourageergedrag van slingerapen verschilt sterk met de seizoenen. Tijdens de 'grote regentijd', als er een overvloed aan rijpe vruchten is, wordt het aktiviteitsbudget verhoogd met als resultaat grotere dagtochten (max. 5.000 meter), grotere kumulatieve eettijden en kortere kumulatieve rusttijden per dag, en de exploitatie van veel meer voedselbronnen (vooral rijpe vruchten) per dag. Er wordt gewoonlijk in relatief grote subgroepen gefourageerd, die regelmatig uiteenvallen en weer fuseren, waarbij de beide subgroepen deels verschillende voedselbronnen kunnen benutten maar ongeveer gelijke routen volgen. Gedurende de 'grote droge tijd', waarin het aanbod van rijpe vruchten laag is en een voedselschaarste of zelfs een voedseltekort kan ontstaan, wordt het aktiviteitsbudget tot een minimum verlaagd, met als resultaat korte dagtochten (min. 500 meter), relatief lange kumulatieve rusttijden en korte kumulatieve eettijden per dag (in de vorm van weinig, relatief lange eetsessies), de exploitatie van weinig voedselbronnen per dag, en een dieetsamenstelling die zich onderscheidt door veel hogere percentages bloemen en jonge bladeren. Tenslotte, neemt ook de gemiddelde subgroep-grootte sterk af.

Slingerapen leven in middelgrote groepen die permanent in wijdverspreide subgroepen van variabele samenstelling uiteenvallen. Dagtochten en aktiviteitspatronen van een subgroep worden gewoonlijk bepaald door een zg. 'dominant' (vaak ouder) vrouwtje met of zonder nakomeling(en), of soms afwisselend door twee 'dominante' vrouwtjes. Deze vrouwtjes blijken ieder bepaalde delen van het woongebied van de groep, de zg. 'core areas', het beste te kennen, en zijn in staat van te voren een ekonomische dagroute te 'plannen' langs 8 tot 30 verschillende voedselbronnen. Door regelmatig het rijpingsstadium van potentiële voedselbronnen te kontroleren en met gebruik van een hoogontwikkeld topografisch en temporeel geheugen zijn 'dominante' vrouwtjes in staat deze voedselbronnen in te passen in hun dagelijkse trekrouten zo gauw deze beschikbaar komen. Het interval tussen twee achtereenvolgende bezoeken aan een bepaalde voedselbron blijkt soortspecifiek te zijn en hangt af van de rijpingssnelheid van de betreffende vruchten. Bij sommige soorten verloopt het laatste rijpingsstadium snel, zodat elke dag voldoende rijpe vruchten beschikbaar komen om samen van te eten. Veel soorten echter worden door een 'dominant' vrouwtje in een 2 - 4 daagse cyclus geëxploiteerd, sommige in een 5 - 8 daagse cyclus of meer. Slingerapen blijken zoveel mogelijk afwisseling aan te brengen in hun dieet en gebruiken gemiddeld ongeveer 14 verschillende voedselitems per dag, een aantal dat ongeveer overeenkomt met 1/4 van het gemiddelde maandelijkse aantal gebruikte voedselitems. Hiervan zijn 3 of 4 items heel belangrijk, wat afgeleid kan worden uit de totale eettijd en het geschatte totale gewicht aan opgenomen voedsel.

6. Een groep zwarte slingerapen bestaat gewoonlijk uit 15 - 20 individuen, welke nooit tegelijk op dezelfde plek kunnen worden waargenomen. Een groep valt permanent uiteen in verscheidene subgroepen van steeds wisselende samenstelling, waarbij een vrouwtje met haar nakomelingschap (dat tot een leeftijd van ongeveer 5 jaar in haar nabijheid verblijft) de enige blijvende band vormt. De sexe-verhouding tussen volwassen mannetjes en vrouwtjes is 1 : 2(-3). De volwassen mannetjes van een groep blijken een duidelijk begrensd territorium te verdedigen, terwijl de vrouwtjes daarentegen naburige groepen kunnen bezoeken en zelfs kunnen emigreren.

De sociale organisatie van de slingeraap wordt gekenmerkt door een flexibel groepeergedrag en lijkt een co-evolutie te hebben doorgemaakt met het voedselspecialisme van de soort, dat in hoofdzaak voedzame, groot-zadige vruchten betreft. Het aanbod van dit voedseltype verschilt sterk met de seizoenen en de rijping in en tussen individuele fructificerende planten verloopt in het algemeen tamelijk traag en asynchroon. Bovendien zijn de individuele vruchten van dit type bij rijpheid gewoonlijk slechts kort beschikbaar voor de apen. De rijpe vruchten vallen meestal spoedig op de bosgrond of in het geval zij met kleppen openspringen (en langer blijven hangen) worden zij ook exploitabel voor vogels. Deze voedselplanten bieden meer dan 3 grote slingerapen zelden genoeg voedsel om samen van te eten en het bezoek te rechtvaardigen in termen van energieverbruik. Bijgevolg worden subgroepen van 3 of minder grote individuen frequenter waargenomen. De hoge dichtheid van bepaalde voedselplanten, die in de 'grote regentijd' fructificeren, maakt het evenwel mogelijk dat slingerapen in veel omvangrijkere subgroepen fourageren, die dan vaak twee 'dominante' vrouwtjes bevatten en tot 9 individuen kunnen tellen. Daarbij volgen de dieren ongeveer dezelfde routen, maar benutten deels verschillende voedselbronnen. In dit seizoen zijn de sociale interacties binnen de groep dan ook sterk toegenomen. In de daaropvolgende 'grote droge tijd', waarin voedzame vruchten schaars zijn en sommige jaren zelfs een ernstig voedseltekort kan bestaan, neemt de gemiddelde subgroep-grootte sterk af, welke afname in het bijzonder teweeggebracht wordt door het opsplitsen van de 'core areas' der 'dominante' vrouwtjes, welke nu bijna geen overlapping meer vertonen. 'Niet-dominante' vrouwtjes en ook mannetjes kunnen zich nog steeds bij subgroepen aansluiten die door een 'dominant' vrouwtje worden geleid, teneinde te delen in haar grotere ecologische kennis van beschikbare voedselbronnen, maar zij doen dit minder frequent. Dagtochten worden opvallend kleiner, de dieren worden zwijgzamer, welke faktoren weer bijdragen aan de geringere ontmoetingskans. Het aktiviteitsbudget wordt verlaagd, vooral bij mannetjes en 'niet-dominante' vrouwtjes. Vooral in de 'grote droge tijd' zijn de 'dominante' vrouwtjes bevoordeeld door hun grotere kennis van de beschikbare voedselbronnen en hun gave ekonomische routen langs deze voedselbronnen te 'plannen'. Dit zou een reden kunnen zijn voor het verschijnsel dat 'dominante' vrouwtjes op grond van een aantal waarnemingen succesvoller lijken te zijn in het grootbrengen van jongen dan 'niet-dominante' vrouwtjes, en dat de mortaliteit bij volwassen mannetjes hoger is dan bij volwassen vrouwtjes. Aan het eind van de 'grote droge tijd', als het aanbod van geprefereerde rijpe vruchten nog klein is, stelt het relatief frequent eten van jonge bladeren en bloemen de slingerapen wederom in staat in grotere subgroepen te fourageren, omdat de uitlopende of bloeiende voedselbomen vaak grote kronen hebben en tegelijkertijd een grote hoeveelheid voedsel bieden.

Volwassen mannetjes bezitten ook 'core areas', die groter zijn dan die der 'dominante' vrouwtjes en welke zelfs de oppervlakte van die van twee 'dominante' vrouwtjes kunnen beslaan. Volwassen mannetjes werken samen bij de verdediging van het territorium door middel van 'grenspatrouilles' en agonistisch afstandsvertoon bij grenskonflikten. Op deze wijze schijnen slingeraapmannetjes méér vrouwtjes te kunnen verdedigen, dan zij zouden kunnen in een sociaal systeem met sterk samenhangende, bisexuele groepen, zoals het geval is bij vele andere primaten.

De sociale organisatie van de slingeraap is ongewoon voor primaten en vertoont alleen opvallende overeenkomsten met die van de chimpansee (Pan troglodytes). Beide soorten zijn grotendeels fructivoor, en vertonen een losse en instabiele sociale struktuur binnen afzonderlijke groepen. De gemiddelde subgroep-grootte varieert seizoensgebonden in relatie tot het voedselaanbod en is gewoonlijk klein. Individuele volwassen dieren bezetten 'core areas' en vertonen het vermogen tot en het voortdurend gebruik van een gedetailleerd, hoog ontwikkeld topografisch geheugen. Voorts vertoont het dominantie- en sexuele gedrag van beide soorten opmerkelijke overeenkomsten.

7. Het woongebied van de groep slingerapen in het studiegebied bij de Voltzberg besloeg 255 ha, waarvan 220 ha geschikt biotoop boden. De dagtochten liepen in lengte uiteen van 500 tot 5.000 meter, afhankelijk van de grootte en kompositie van de gevolgde subgroep, het weer, het seizoen en de verspreiding van bepaalde belangrijke voedselbronnen. In het Voltzberggebied komt Ateles paniscus paniscus voor in een dichtheid van 7.1 individuen per km^2, of 8.2 individuen per km^2 wanneer alleen geschikt biotoop in aanmerking genomen wordt. De biomassa bedraagt 0.4 tot 0.5 kg/ha, afhankelijk van de gekozen omvang voor het woongebied.

Ateles vertoonde geen polyspecifieke associaties met andere sympatrische primatesoorten. Kortstondige associaties waren meestal het gevolg van toeval, terwijl sommige waargenomen associaties moeten worden beschouwd als louter vriendschap. Associaties met terrestrische vogels en zoogdieren, evenwel, zijn vaak waargenomen en kunnen voor één of meer deelnemende soorten van nut zijn. De terrestrische dieren worden aangetrokken door de luidruchtig fouragerende slingerapen en kunnen zo voedzame vruchten en/of zaden bemachtigen onmiddelijk nadat deze op de grond gevallen zijn, terwijl de alarmkreten van vluchtende dieren op de grond de slingerapen kunnen waarschuwen voor mogelijke indringers in het gebied.

8. Slingerapen zijn uiterst kwetsbaar met betrekking tot jacht en biotoopvernietiging. Zij verdwijnen overal in hun verspreidingsgebied zodra de mens op het toneel verschijnt en vertonen weinig of geen adaptatievermogen ten aanzien van storingen door de mens. Met de nadruk op de belangrijke rol die 'gespecialiseerde' fructivoren, zoals slingerapen, als verspreiders spelen voor vele planten van het tropische regenwoud, èn op het evenwicht tussen zaadverspreiders en zaad- en zaailingpredatoren zoals die interakties aangaan met vruchten, welk evenwicht een belangrijke uitwerking heeft op de opbouw en samenstelling van het ongestoorde tropische regenwoud, wordt een suggestie gedaan de belangen van zowel natuurbeschermers als commerciële exploiteurs van regenwoudschatten te verenigen in natuurbeschermingsprojekten. Als voorbeeld moge dienen de verantwoorde exploitatie van bufferzones rondom nationale parken en natuurreservaten door daar de dichtheden van bepaalde voor commerciële houtkap waardevolle èn eetbaar-fruit producerende bomen te verhogen en een beperkte jacht toe te staan op terrestrische zaadpredaterende dieren en herbivoren, zoals bijv. agoeti's, paca's, peccaries, herten en tapir's.

CONTENTS

Acknowledgements

1. INTRODUCTION

2. METHODS

3. HABITAT PREFERENCES

4. DIET

5. FEEDING BEHAVIOUR

6. DIET, FEEDING STRATEGY AND SOCIAL ORGANIZATION

7. POPULATION DYNAMICS

Acknowledgements

I am indebted to a number of people, who made this study possible. First of all I would very like to express my thanks to my friend and colleague Dr. Russell A. Mittermeier, who introduced me in the tropical rain forest and in the world of Surinam monkeys. Together, we set up an area for studying the synecology of Surinam primates, with some additional work later on adapted by myself to conduct an autecological study on spider monkeys. His assistance in the field during part of the study and his valuable discussions and critical comments, also during the analysis and writing up of the results, have been essential for my work.

Furthermore, special thanks are due to Dr. Anne van Wijngaarden, who supervised the project in all stages, for his practical advice and encouragement and for contributing many useful comments.
Without the continual support of these two people the project could never have been carried out.

I also wish to tender my sincere thanks to Prof. M. F. Mörzer Bruyns and Prof. C. W. Stortenbeker of the Agricultury University, Wageningen, and to Dr. J. C. Lindeman of the Institute of Systematic Botany, Utrecht, for their constructively critical comments on the draft of the manuscript.

Many thanks to Dr. Paul J. M. Maas for supervising and stimulating my work on the fruits of Surinam, that provided a firm base for the study on diet in Surinam monkeys. Also, thanks are due to several other botanists of the Institute of Systematic Botany, Utrecht, who helped me in identifying food samples of rare species.

Thanks are also extended to Dr. A. Gentry of the Missouri Botanical Garden for naming several samples of rare Bignoniaceae; to Dr. N. Duplaix and P. Teunissen for locality data and other information on spider monkeys; to B. de Jong and T. Holthuyzen for providing an initial vegetation map of the study area; to M. Werkhoven and Dr. J. C. Lindeman for information on Surinam forest types and plant species; to the Surinam Geological Services for transportation and lodging in the Kayser Mountains, where I did a survey using their trail system; to P. Loth for assisting me in the field during the last seven months; to F. van Troon, tree-specialist of Dienst 's Lands Bosbeheer, for marking about 10.000 trees and lianes in the study area.

I am greatly indebted to my Surinam bushnegro and amerindian friends and their children on Foengoe Island, Raleighvallen, who provided us, in particular my wife and son, a very pleasant atmosphere to live in between during the course of the field study.

Many thanks go to A. Griffioen, the artist of the Research Institute for Nature Management, Leersum, for his original interpretation and outstanding realization of the histograms and maps.

I shall always be indebted to my wife Betty, for the unselfish contribution she has made to every aspect of this long study. Moreover, most drawings of food items are made by her in the field.

Finally, I would like to express my appreciation to F. Baal of Stinasu (Surinam Nature Conservation Foundation) for permission to work in the Raleighvallen-Voltzberg Nature Reserve and for his personal interest in this study.

This field study of the black spider monkey was financed by the Netherlands Foundation for the Advancement of Tropical Research, The Hague. Departmental facilities were kindly provided by the Research Institute for Nature Management, the Institute of Systematic Botany and the Agricultury University.

1. INTRODUCTION

1.1. Background

One of the topics in recent literature on the behaviour of free-ranging primates is to investigate food as one of the basic determinants of social organisation and behaviour. However, very detailed autecological studies on undisturbed primate populations, urgently needed for this investigation, unfortunately are few. One of the main reasons may be the fact that primatology and botany seem to be a rare combination of skills. The floristic complexity of the oldest terrestrial ecosystem on earth, the tropical rain forest, surely will play a role. Considering this before starting this field study, I compiled all available data on fruits and seeds of woody plants of Surinam, in the knowledge that all Surinam monkeys are, at least for a considerable part, frugivorous. Research of two years resulted in a book ('Surinaams Vruchtenboek', 1977), with detailed descriptions of the fruits and seeds of about 1400 species of trees and lianes. A drawing of most of them was included, besides general descriptions of leaves and inflorescences of the species, habit of the plant and habitat preferences. It turned out to be a useful book to identify most food plants right in the field. Monkeys at least drop parts of fruits and sooner or later whole fruits, sometimes with leaves attached, while trees and lianes usually drop their fruits in a certain stage of maturity, making the collecting of fruits much easier than that of flowers and leaves. The identification of species in the field on fresh samples will increase one's knowledge of the forest incomparably much faster than the usual way of collecting, preserving, shipping and much later on naming of the samples. Learning about the plants, while studying monkeys, will be of great advantage. Types and subtypes of forest are easier to recognize by determining and recognizing certain indicator species. The undrestanding of the forest will be better, not walking anymore in an indiscriminated mass of trunks and stems. By fixing in one's memory special properties of individual trees of known species, one will become habituated to every spot of the forest visited once or more times before. All attention can be directed to the monkey's behaviour from now on. Also the phenology of forest plants will be easier to study by collecting all kinds of fresh fruit from the forest floor from month to month in successive years. In this way periodicity and length of fruiting period can be determined for many species.

This study recognizes the fundamental importance of food to spider monkey behaviour and population dynamics. It clears up the complex temporal and spatial effects of food sources on the behaviour of a group of spider monkeys in terms of food category, food plant identity and phenology, and in terms of quantity, density and dispersion of the most important of these food sources. Besides this, the present study describes habitat choice and feeding strategy, and it discusses implications of diet to social behaviour in Surinam black spider monkeys (*Ateles paniscus paniscus*).

Till today, very few data were available on diet and habitat choice of *Ateles p. paniscus*. Some more is known about two other species, *Ateles belzebuth* and *Ateles geoffroyi*. C.R. Carpenter (1935) reported on a natural population of *A. geoffroyi* in Panama. He described the species as frugivorous. About 90% of the items they consumed were said to be fruits. Few data on other food stuff were reported by Carpenter.
In 1969, Hladik and Hladik descibed feeding behaviour, diet and quantitative and chemical analyses of many food items used by a group of *A. geoffroyi*, reintegrated since 1961 on Barro Colorado Island, Canal Zone.
Klein and Klein observed *A. belzebuth* in the Colombian National Park, La Macarena, during one year (1967 - 1968). Among other things, they inform on diet, feeding behaviour, feeding heights and sites and social organisation (1972, 1976, 1977).

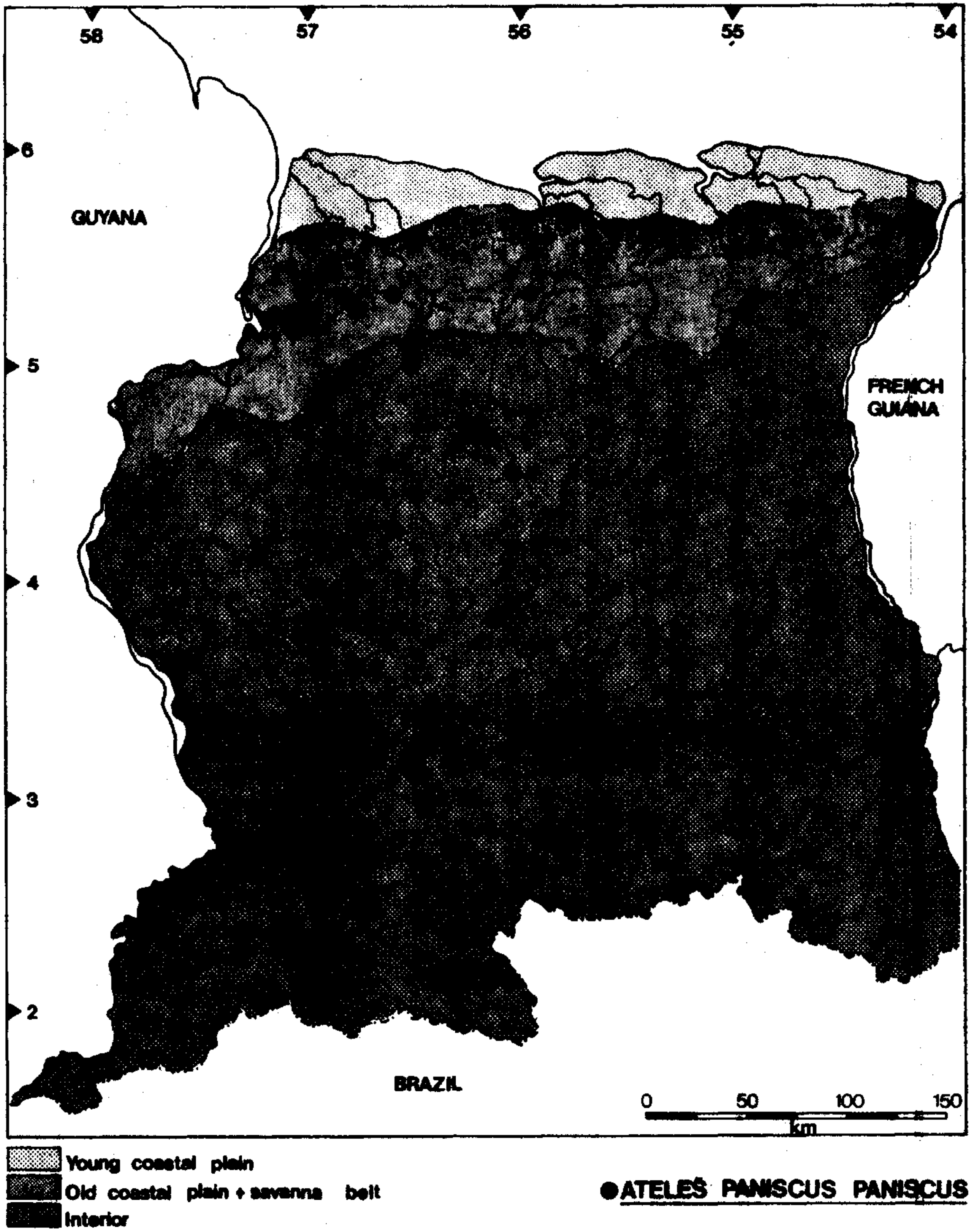


Fig. 1. Distribution map for Ateles paniscus paniscus in Surinam. The heavy unbroken line marks the border between the coastal region and the interior. The area immediately to the north of this line is the old coastal plain, that to the south is the savanna belt. The dashed lines indicate the borders of the two areas. For the purposes of this study, the savanna belt is considered part of the interior, but it is actually a geologically distinct region. Ateles occurs throughout the interior, but is rare in the savanna belt and only enters the old coastal plain in the extreme western part of the country.

Apart from the aims described already, this study is fundamental from a conservational point of view. *Ateles* is probably the most vulnerable of the Surinam monkey species. It is large and noisy and can be easily tracked and hunted. In undisturbed areas they usually react to a human intruder by performing a 'branch shaking and branch dropping display', attracting also other subgroups. A hunter can wipe out whole groups with little effort. Moreover, *Ateles* is largely restricted to undisturbed high forest, and consequently habitat destruction has more effect on it than on other species. Another important point is its slow reproductive rate. Usually a female gives birth only once in 3 or 4 years. This means that the species is poorly adapted to recover from exploitation.

In order to implement proper measures for conservation, data on forest type preferences and diet of species, that are to be protected, are essential tools for assessing the potential of proposed protected areas. In order to assess the site in the first place, one needs ecological data on the primates that are to be protected, or on closely related species.

1.2. Taxonomy and Distribution of Ateles

The taxonomy of the genus *Ateles* is the subject of some controversy. Kellogg and Goldman (1944) recognize four species of *Ateles*: *A. geoffroyi*, *A. fusciceps*, *A. belzebuth* and *A. paniscus*. Several recent authors (e.g., Hershkovitz, 1972; Groves, 1972; Moynihan, 1970, 1976), however, consider all *Ateles* conspecific and refer to them collectively as *A. paniscus* (the oldest available name). Recent studies indicate that there may be some significant chromosome differences among the species recognized by Kellogg and Goldman (Heltne and Kunkel, 1975). Furthermore, an important contact zone between *A. geoffroyi* and *A. fusciceps* exists in eastern Panama and the species apparently hybridize to some extent (Rossan and Baerg, 1977). Until further information becomes available, I prefer to follow Kellogg and Goldman (1944) and use the name *Ateles paniscus* in the strict sense.

The Surinam representative of the genus is *Ateles paniscus paniscus* Linnaeus, 1758. It is found in lower Amazonia, between the Rio Negro and the Atlantic and north to the Guianas (Kellogg and Goldman, 1944), a range similar to that of *Saguinus midas midas*, *Pithecia pithecia*, *Chiropotes satanas chiropotes* and *Cebus nigrivittatus*, four of the other seven primate species occurring in Surinam.

The second *A. paniscus* subspecies, *A. p. chamek*, is found in western Matto Grosso, eastern Bolivia and northeastern Peru and extends into Brazil as far east as the Rio Jurua, a southern tributary of the Rio Amazonas (Kellogg and Goldman, 1944). The other three species of *Ateles* are found from Southern Mexico to the southern reaches of the Amazon basin.

In Surinam, *A. p. paniscus* is almost entirely restricted to the interior. Like *Chiropotes s. chiropotes* and *Cebus nigrivittatus*, it just enters the old coastal plain in the western part of the country (Fig. 1).

Ateles p. paniscus is covered with long, glossy black hair. The naked face varies from light to dark pink and is sometimes lightly freckled. The eyes are usually brown, but some individuals have blue eyes. The female has a long pendulous, backward-directed clitoris, that immediately distinguishes her in the field. The scrotum of the male is black.

The hair on the head in both sexes is long and directed forward, forming a peak over the eyes. Individual differences in face colour and marking, eye colour, hairtuft, hair length and physique make them after a while quite well recognizable in the field, even at high distances.

Ateles p. paniscus is a large monkey. It is slightly dimorphic in size. Five males weighed in Surinam had a mean weight of 7.86 kg and seven females a mean weight of 7.70 kg (Mittermeier, 1977).

1.3. Climate

Surinam lies close to the equator and has a typical tropical climate.

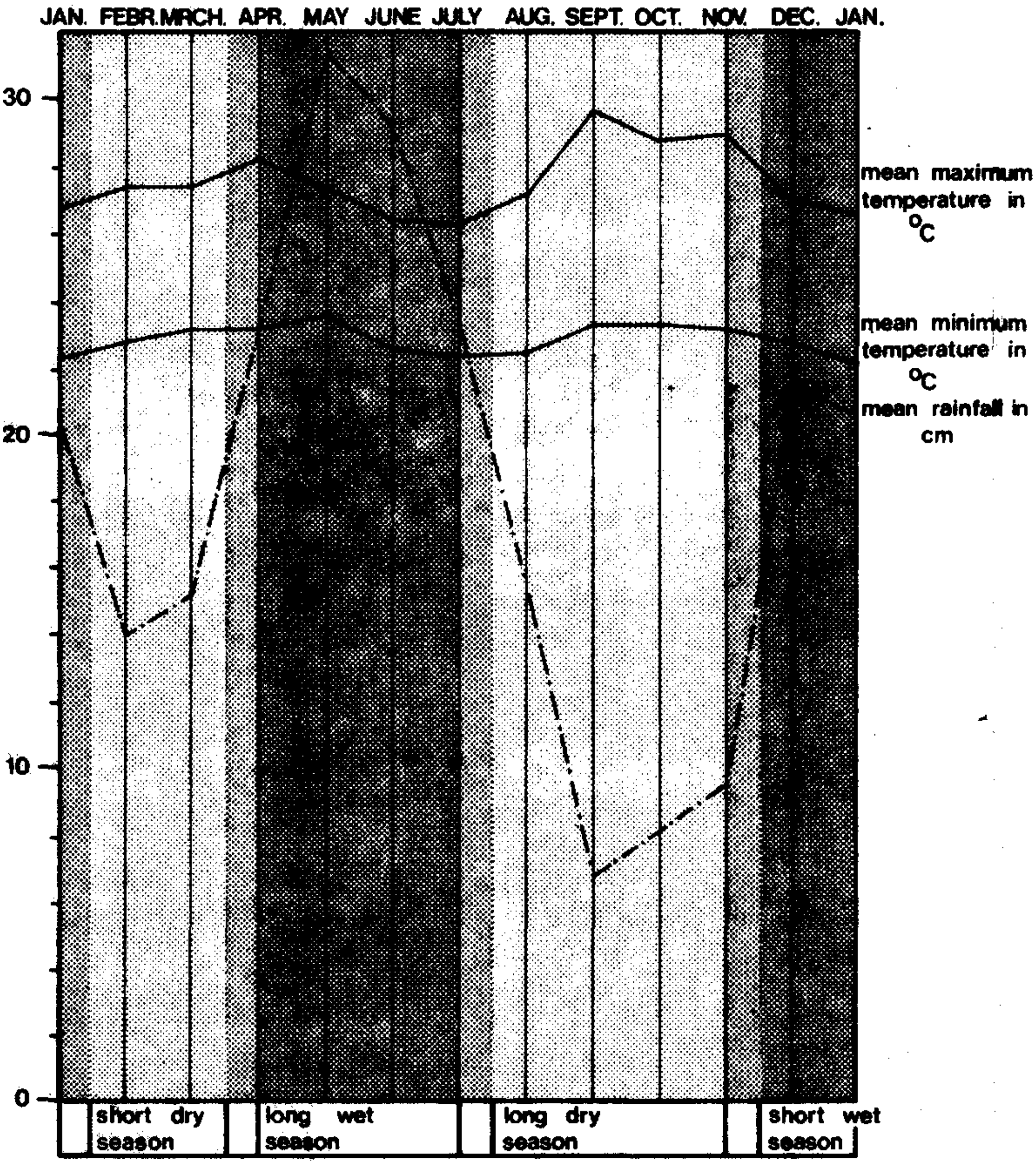


Fig. 2. Climate of the Voltzberg study area during the present study, showing the mean monthly variations of maximum and minimum temperature at 1.5 m in the rain forest (full lines) and rainfall in a clearing (broken line) (data collected from May 1976 to May 1978).

The mean annual temperature is 26.1°C (Lindeman and Moolenaar, 1959). Mean monthly temperatures vary only about 2° during the year. A maximum is reached in September and October and a minimum in January and February. Daily variations are greater and range from 21.0 - 31.6°C at 1.5 m in the rain forest. Temperatures at the top of the canopy are similar to that in clearings and range from 21.0 - 36.0°C.
Personally collected data over two years, at 1.5 m in the rain forest in the Voltzberg study area, show temperature maxima in September, October and November and minima in June, July and January (Fig. 2).

Relative humidity in the rain forest is highest in the early morning (95% or more), drops to about 82% during the middle of the day and reaches 95% again at dusk. In clearings and at the top of the canopy the daily range is greater and humidity may be as low as 40% in the middle of the day (Schulz, 1960; Hoogmoed, 1969).

Mean annual precipitation lies between 2000 and 2400 mm (Lindeman and Moolenaar, 1959) and is not evenly distributed throughout the year. Usually four seasons are recognized. A long wet season, usually beginning in mid-April and lasting until mid-July, with a maximum rainfall in May or June. A long dry season begins in August and lasts until mid-November. October is, in the average, the driest month, but differs only slightly with September. The period from December to April can be divided into a short wet and a short dry season that vary much in intensity. The short wet season usually runs from December to January or February, the short dry season from February to March or April. In abnormal years one of the two can be absent. In 1976 the long dry season lasted from August to February 15th, 1977. After a very short wet period of two weeks, a short dry season of 1½ months followed, while the long wet season started about April 15th.
The long dry season is characterized by a monthly rainfall of less than 100 mm. October is the driest month with as little as 20 mm locally (Hoogmoed, 1969). May is usually the wettest, with precipitation that may exceed 400 mm locally. During the two years of observation in the Voltzberg study area, the driest month was September with precipitation as low as 68 mm. The wettest month was May with 316 mm (Fig. 2).

The nights in the interior are mostly windless. Gales are rare. Like elsewhere in the tropics the most violent winds are squalls. They occur particularly during the transition periods (especially in July and August) and may precede thunderstorms. During such squalls it is risky to walk through the forest. Everywhere trees can be heard falling, old but also vigurous, especially during and just after heavy rainfall. This phenomenon is of great importance for the regeneration of mature forest.

1.4. Geology

The interior of Surinam is a part of the Guyana Shield, a formation of Precambrian age, that is composed mainly of granito-diorites and granites. In central Surinam a single remnant of the Mesozoic Roraima sandstones, the Tafelberg, has withstood erosion. The rocks in the interior are usually covered with deeply weathered ferrosiallitic/ferrallitic soils that vary from loamy sand to clay. Here, one finds high upland forest. On shallow soils covering laterite caps and outcrops of unweathered granite, one finds more or less xeromorphic types of vegetation (Bakker, 1957). In some areas like the Voltzberg region exposed, unweathered rock can still be seen at the surface. These granite-inselbergs are mainly covered with Lichens and Algae. These cause weathering with high PH-values. The SiO_2, dissolved under these circumstances, is deposited in the form of small, very resistant sheets. Together with the Lichens and Algae, the SiO_2-sheets shut the granite off from deeper weathering, a process which seems to be essential for the forming of inselbergs in the tropics (Bakker, 1957).

1.5. Topography

The coastal region of Surinam has almost no accentuation. In the interior several low mountain ranges are found, the highest peak being 1280 m (Wilhelmina Mountains). Several plateaus, like the Brownsberg (514 m), are given mountain status in Surinam, and also isolated outcroppings like the Voltzberg (240 m) and the Van Stockumberg (360 m).

Six major rivers dissect the country and for the most part flow from south to north. The Corantyne forms the border between Surinam and Guyana, the Marowijne divides Surinam and French Guiana.
The lower reaches of the rivers are calm, but the upper reachs below 5° N are broken by many rapids (e.g., the Raleighvallen-complex in the Coppename River near the Voltzberg).

1.6. Vegetation of Surinam

The Surinam coast primarily consists of mudflats covered by mangroves and broken by occasional beaches. Behind these lies a large stretch of swamps, cut by sand and shell ridges running parallel to the coast. Moving further south, there is a belt of rain and marsh forests, then a narrow belt of white sand savannas and savanna forests, and finally the rain forests of the interior (Hoogmoed, 1969). The savanna belt, which begins roughly 25 km from the coast in the east and 80 km in the west, is not part of the coastal region and can be considered a division of its own or part of the interior. The interior is for the most part covered with high tropical rain forest broken by other forest types and small savanna enclaves. The largest of these is the Sipaliwini Savanna, which is located in the extreme south and connected with the larger Paru Savanna of Brazil.

1.7. Structural Description of the Forest Types found in the Raleighvallen-Voltzberg Region

1.7.1. DRY EVERGREEN FOREST TYPES

Tropical Rain Forest

High rain forest. The range of forest types in Surinam covers Beard's (1955) categories of true tropical rain forest and evergreen seasonal forest. Because a continuum exists between the two categories, it is preferred to follow Lindeman and Moolenaar (1959) and Richards (1952) in using the term high rain forest or high dryland forest to include the two Beard types.

High forest is found in areas not affected by seasonal flooding of rivers, The soil varies from loamy sand to clay, drainage is fair to good and litter decomposition is good. Usually it is possible to distinguish three to four storeys in high forest. The upper storey consists of emergent trees which can reach 40 - 50 m and very rarely more (in Surinam only Cedrelinga cateniformis reaches locally 60 m). Below the emergents is the canopy, which ranges from 15 - 30 m and can itself be divided into three categories, the upper part (25 - 30 m), the middle part (20 - 25 m) and the lower part (15 - 20 m). The understory consists of slender trees up to about 15 m, while saplings and undergrowth species make up the bottom 3 m.
In general, the crowns of the emergent trees are wider than deep and spread over the lower trees around them. No lianes connect them with the canopy crowns. The canopy crowns are almost as wide as deep and many lianes connect them, whereas those of the understory vary from long and narrow to tapering. Many species of lianes (some important families are Bignoniaceae, Celastraceae, Convolvulaceae, Leguminosae and Menispermaceae) occur in high forest, but individually they are mostly widely dispersed. Epiphytes, like many Araceae, Bromeliaceae and Orchidaceae, occur mainly in the crowns of

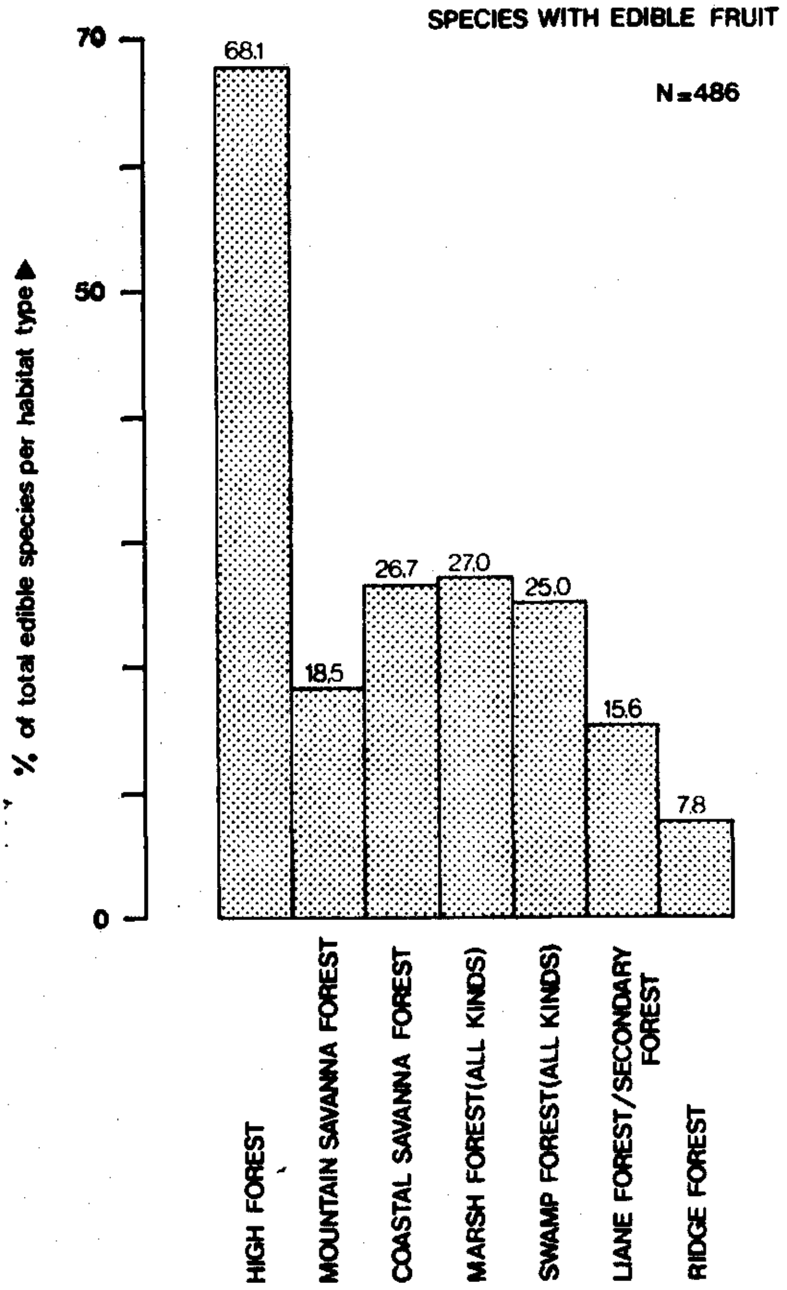


Fig. 3. Woody plant species with edible fruit and growing to at least 2 meters in height, the families Araceae and Palmae not included, in high forest and several other forest types in Surinam. High forest has far more edible fruits than any other formation (data on edibility are taken from Van Roosmalen's 'Surinaams Vruchtenboek').

trees. Stilt roots are rare, but buttresses are common. The herb layer is very open and consists mainly of broad-leaved forest grasses, small saprophytes and shrubby Rubiaceae. Palms are common in high forest. Oenocarpus bacaba reaches the canopy, while Astrocaryum, Attalea and Bactris are found in the understory (Lindeman and Moolenaar, 1959).

High forest is very rich in species and it seldom shows any tendency to single-species dominance. The abundance of species makes it difficult to characterize high forest floristically. In the present study, the floristic composition of high forest and high mountain savanna forest in the Voltzberg region is partly analysed by means of ½ ha plots, taking into account only tree and liane species important for Ateles. The most important vegetational attributes measured were number and distribution of the component plants. The most decisive criterion for an evaluation of the relative importance of a species in a given forest stand is the number of individuals. That they have succeeded in the struggle for existence is shown by reaching the reproductive state. One will see that the composition of the forest shows distinct variations from place to place. Some species show a wide ecological amplitude, others do not and are more local.

As demonstrated in Fig. 3, high forest has far more species producing edible fruit than any other formation. Of a total of 486 edible species recorded for Surinam, 331 are found in high forest. Consequently, high forest is the most important primate habitat in Surinam. All eight primate species occur in high forest and several (Chiropotes, Cebus nigrivittatus and Ateles) are largely restricted to this formation.

The high forest of the Voltzberg region seems to offer a somewhat poorer appearance than the lowland rain forest in its optimal development. In general, the lower part of the canopy and the undergrowth are poorer in species, perhaps due to the abundance of boegroemaka palms (Astrocaryum sciophilum), that locally form a fairly continuous layer at about 8 m height. The ground flora is very sparse. Young acaulescent boegroemaka palms locally dominate and together with the old palms, with a well-developed heavily armed trunk up to 5 m and sometimes even up to 12 m, they effectively intercept the light. When experienced in cutting off in the right way some leaves of the armed young boegroemaka palms, one can walk very fast through this type of forest, an important factor to make the following of fast moving monkeys like Ateles possible. Moreover, it makes it easy to find one's way back or to trace a route of monkeys followed earlier. The silvery underside of cut palm leaves marks the trail as a silvery string through the forest.

Low rain forest. This term is used to designate a type of high forest that does not exceed 20 m in height. It is far richer in lianes than neighbouring high forest, and has far fewer boegroemaka palms. Usually, it forms a transition between high forest and liane forest, and sometimes mountain savanna forest. It isn't drawn on the vegetation map (Fig. 6) because it usually covers only small strips along part of the above mentioned margins.

Riverbank high forest. Riverbank high forest is absent from most of the coastal region, but it is common in the interior. In areas where river banks are high and not affected by seasonal flooding of river margins, riverbank high forest may grow right up to the river's edge. This kind of forest should not be confused with marsh forest since the soil is rarely or never inundated. The structure of riverbank high forest is very similar to that of inland high forest, but the composition is clearly different. A continuum seems to exist, but in the Raleighvallen study area I determined several indicator species for riverbank high forest in this region, which disappear about 700 m inland. Examples are the understory tree species Palicourea guianensis (Rubiaceae), the liane Cheiloclinium cf. gleasonianum (Celastraceae), an Eugenia species (Myrtaceae), and the tree species *Vouacapoua americana* (Caesalpiniaceae). Because the Voltzberg study area began almost 2 km from the bank of the Coppename River, this forest type was not present there.

Mountain Savanna Forest

Mountain savanna forest occurs on bauxite hills and low mountains where only a thin layer of soil covers the underlying rock. It is similar to savanna forest on white sand in xeromorphy, thin-stemmed aspect, coriaceous structure of leaves and lack of clear differentiation into storeys (it has a rather regular canopy of small crowns with few emergents), but it differs in floristic composition. Lianes are common, but not nearly as common as in formations like liane forest. Understory palms like *boegroemaka* (*Astrocaryum sciophilum*) are conspicuously absent. The undergrowth consists mainly of shrubs and treelets of Rubiaceae and Myrtaceae, easily to walk through. Visibility is much better than in high forest.

The dominant plant families in mountain savanna forest are Myrtaceae, Sapotaceae and Rubiaceae, which include several important fruit-producing trees for monkeys. In total, 90 species of trees and lianes producing edible fruit have been recorded from mountain savanna forest (Fig. 3).

A high mountain savanna forest formation, intermediate between typical mountain savanna forest and high rain forest, sometimes occurs on more favourable parts of the bauxite plateaus and in granite areas like those surrounding the Voltzberg and the Van Stockumberg in the Upper Coppename region. Some of the dominant species in this formation are *Ecclinusa guianensis* (Sapotaceae), *Guettarda acreana* (Rubiaceae), *Lafoensia pacari* (Lythraceae) and *Pterocarpus* vs. *santalinoides* (Papilionaceae). At edges of high mountain savanna forest one frequently finds important food trees for monkeys such as *Ceiba pentandra* (Bombacaceae), *Hymenaea courbaril* (Caesalpiniaceae) and *Spondias mombin* (Anacardiaceae).

During extremely dry seasons (like in 1976), most of the mountain savanna forest trees drop their leaves giving the forest a dead appearance, but in normal years only part of the trees seems to be deciduous.

Liane Forest

Liane forest is a formation in areas with stony lateritic soils providing bad rooting conditions and poor foothold for trees. It is noteworthy for the absence of storeys. Tall trees do occur, but they are so widely separated from one another that no true canopy exists. The space between the trees is filled with dense tangles of lianes, vines and twiners that grow in abundance because of unrestricted exposure to sunlight. Although occasional tall trees in liane forest may reach 30 m or more, the liane tangle itself rarely exceeds 10 - 15 m.

A large number of species are represented in liane forest, but most of them are of very low frequency. A total of 76 species producing edible fruit have been recorded from liane forest. Of these the most important for monkeys are *Pourouma guianensis* (Moraceae), *Cecropia* spp. (Moraceae) and *Inga* spp. (Mimosaceae). The dense liane tangles provide many microhabitats for insects and other arthropods, making them a fertile foraging ground for partly insectivorous monkeys like *Saimiri* and *Cebus*.

It is not clear how liane forest arises. According to my own observations in the Voltzberg region, it seems to be a degenerated type of mountain savanna forest. Natural clearings in mountain savanna forest, caused by treefalls during squalls or spontaneously, mostly spread over a much larger area than treefalls usually do in high rain forest, probably because of bad rooting conditions. Several of these clearings, which were followed for more than two years after their appearance, were then overgrown by tangles of lianes, vines and twiners, whereas no saplings of successor plants (pioneers) like *Cecropia* spp., *Jacaranda copaia*, *Goupia glabra* and *Laetia procera*, so common in natural clearings in high forest, were seen. More evidence for considering liane forest to be a degenerated type of mountain savanna forest is given by the presence of very old tall trees of *Vitex stahelii* (Verbenaceae) amidst extensive liane forest complexes. It is a typical mountain savanna forest species, apparently offering much longer resistance to heat, light, overgrowing liane masses and wind than any other tree species from mountain savanna forest.

At least in some cases, the low rain forest as mentioned above has to be considered a regenerating type of mountain savanna forest. Trees like *Pourouma guianensis*, *Cecropia surinamensis*, *Inga edulis* and *Inga alba* seem to play an important role in the process of regeneration. At the moment, it is not clear whether liane forest in the Voltzberg region is increasing its area. Detailed study on aerial photographs over long periods is needed to give insight in this matter.

1.7.2. WET FOREST TYPES

Swamp Forest

Following Beard (1955), the term swamp forest is used for forests on soil which stays soaked to wet throughout the year and as a result aeration is permanently impeded. Swamp forest soils are actually under water most of the year and, if not inundated, at least remain damp during the peak of the dry season. The soil is usually composed of heavy clays and litter. The litter decomposes poorly because of bad aeration and accumulates to form a peat layer.

In the Voltzberg-Raleighvallen region only one type of swamp forest is present along the small creeks and streams that flow almost all year round. Because of dominance of the *pina* palm, *Euterpe oleracea*, which locally forms pure stands, it is called *pina swamp* (Plate 11).
Pina swamp forest reaches at least 20 m in height and, because of scattered tall trees, it cannot be differentiated clearly into storeys.
The irregular canopy ranges from 18 - 30 m and is characterized by trees like the buttressed *Virola surinamensis* (Myristicaceae) and *Pterocarpus officinalis* (Papilionaceae), the stilt-rooted *Symphonia globulifera* (Guttiferae), and *Bombax spectabile* (Bombacaceae) and *Eperua falcata* (Caesalpiniaceae), all of which are food plants of *Ateles*. On the aerial photographs one sees a dark background of *pina* palm crowns with a pattern of scattered light-coloured tree crowns of these and some other species. The most common tree is *Euterpe oleracea* itself, reaching the canopy. *Astrocaryum sciophilum* is common, especially on drier places. Visibility is good since the undergrowth is open, formed by relatively few saplings of the above mentioned species and *Euterpe oleracea* itself. Locally a dense herb layer can be present, which can hinder progress.

A total of 122 tree and liane species producing edible fruit have been recorded from the various kinds of swamp forest, but pina swamp forest alone is rather poor in edible species (Fig. 3).

Marsh Forest (Seasonal Swamp Forest)

Marsh forest or seasonal swamp forest in Beard's (1955) terminology is the term used for a number of two-storey forest types whose soils are periodically, but not permanently, inundated during the year (the Brazilian term *várzea* covers several kinds of marsh forest, but other seasonally flooded non-várzea forests also fall under marsh forest). In drier parts of the year they lie above the ground water table, making aeration possible. However, even during the driest months, marsh forests are not subjected to the severe dessiccation that some forms of savanna forest must undergo (Lindeman and Moolenaar, 1959).

The only type of marsh forest occurring in the Voltzberg-Raleighvallen region is *riverbank marsh forest*.

Riverbank marsh forest. This type of forest occurs along river margins and is seasonally flooded by rising waters. The maripa palm, Attalea regia, can be regarded as a good indicator for all types of marsh vegetation. Pentaclethra macroloba (Mimosaceae), Pithecellobium cauliflorum (Mimosaceae), Hymenaea courbaril (Caesalpiniaceae) and Eperua rubiginosa (Caesalpiniaceae) are differentiating species. Triplaris surinamensis (Polygonaceae), Ceiba pentandra (Bombacaceae) and Tabebuia serratifolia (Bignoniaceae) are often common. Palms like Attalea regia and several Bactris spp. can dominate locally to create 'palm forests'.

Marsh forest is rich in species, but of all edible fruit producing tree and liane species recorded, only 27% (131 species) is found in marsh forest. Marsh forest is an important habitat for several monkey species. Especially the dense, liane-covered lower storeys along river margins provide excellent foraging grounds for the partly insectivorous species, like Saimiri sciureus.

1.7.3. XEROMORPHIC VEGETATION

Rocksavanna

Rocksavanna is a rare vegetation type found in the Voltzberg region only on granite where the rock is bare or covered by shallow soil. It consists of bushes, terrestrial epiphytes, cacti and grasses. No palms occur, but some thin lianes and twiners are present. Maximal height is 5 m. The vegetation is not closed. Most common species of bushes are Clusia panapanari (Guttiferae/Clusiaceae), Clusia nemorosa and Ficus pertusa (Moraceae). At edges an important edible fruit producing tree, Spondias mombin (Anacardiaceae), can be found.

This vegetation type is not important for monkeys. Only Saimiri sciureus and Cebus apella sometimes enter it, especially when Ficuspertusa or Spondias mombin is fruiting.

2. METHODS

2.1. The Study Area

The present study was conducted in the Raleighvallen-Voltzberg Nature Reserve, a protected area of 56.000 ha that was established in 1961 and is currently managed by Stinasu, the Surinam Nature Conservation Foundation. It is located on the east bank of the Coppename River in central Surinam (Fig. 4) and is bordered on the north by the Kwama Creek and on the south by the Tanjimama Creek (Fig. 5). It includes Raleighvallen, the boulder-strewn rapids and falls that mark the limit of navigability of the Coppename River and several granitic 'inselbergs', most notably the 240 m dome-shaped Voltzberg and the Van Stockumberg.
The headquarters of the Raleighvallen-Voltzberg Nature Reserve are on Foengoe Island, situated at the lower end of the Raleighvallen rapids. The island can be reached by plane or by boat. A three-hours trip by car or bus, followed by a three to five-hours trip by motorized dugout-canoe brings a visitor to Foengoe, situated about 6 km from the Voltzberg. It has restricted facilities for tourists and researchers and served as a main base during the study.

In March 1976, together with R.A. Mittermeier, a detailed reconnaissance was carried out and the borders of the Voltzberg Study Area were established. Together with several Surinam field assistants, we cut a grid of main trails at 500 m intervals, totalling 15.5 km. In the 130 ha surrounding our camp, at the edge of a big granite plate, we cut an additional 11.2 km of side trails at 100 m intervals, parallel to the long axis of the area, because this part seemed to be important for a group of spider monkeys.

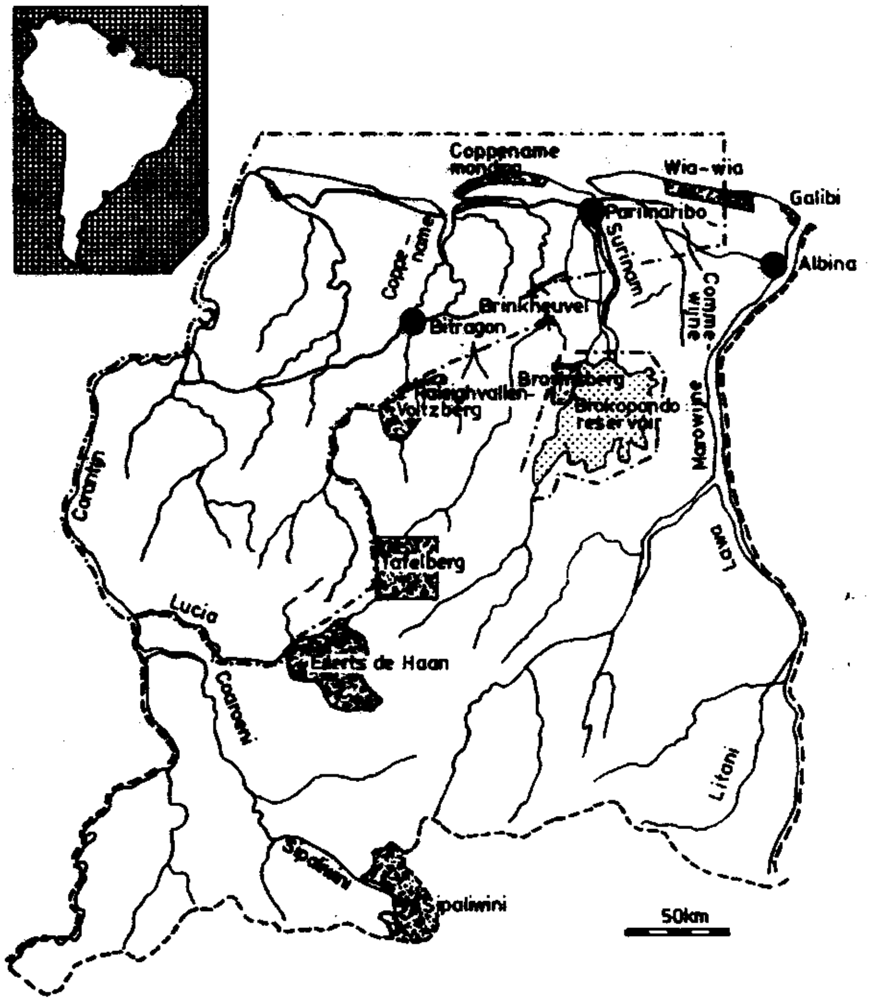


Fig. 4. Map of Surinam showing the location of the Raleighvallen-Voltzberg Nature Reserve and the eight other protected areas in the country.

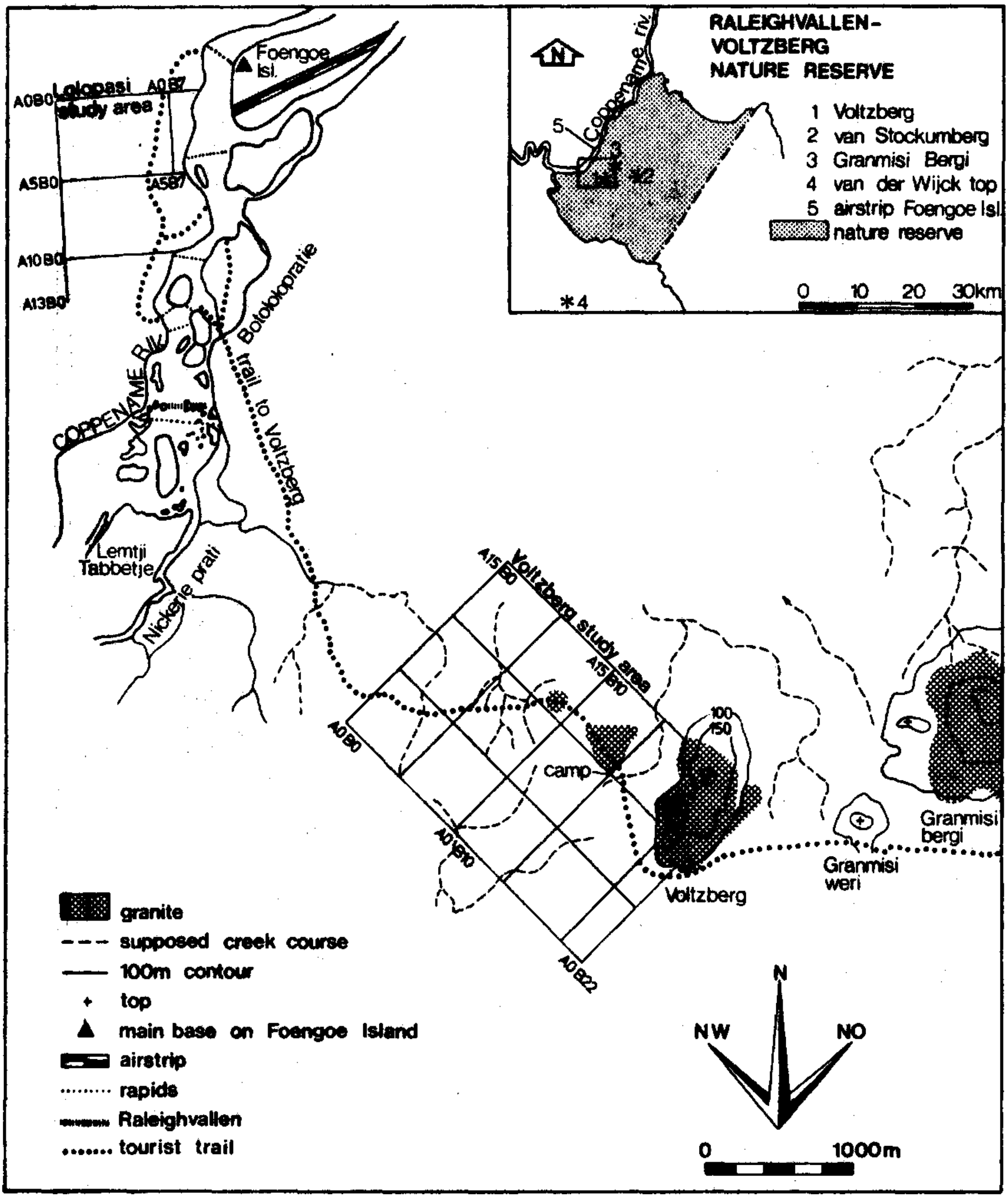


Fig. 5. Map showing the location of both study areas in the Raleighvallen-Voltzberg Nature Reserve. The trail system of the Lolopasi study area has not been completed, since the group of spider monkeys living in the area appeared to be hard to follow and no progression in the habituation could be made. The reason might have been light hunting pressure in the recent past. The main study area at the foot of the Voltzberg dome only shows major trails at 500 m intervals. Smaller connecting trails at 100 m intervals in the B10 - B22 area are not drawn on this map.

The study area consisted of 10 blocks of 25 ha each, two incomplete blocks limited by the Voltzberg and together covering about 44 ha, and a final section of about 12 ha extending the study area to the start of the main trail for visitors ascending the Voltzberg (Fig. 5). When the surface of the two large, open granite clearings in the study area is subtracted, the total forested habitat was almost exactly 300 ha. This study area was used during the first year for gathering synecological data on all eight Surinam primates. In the meantime, I selected a group of spider monkeys and determined very roughly the boundaries of its home range. It soon became evident that the original study area had to be extended with approximately 15 ha to the northeast and 25 ha to the southwest, to cover the whole range of the group (Fig. 6).

All 500 m and 100 m trails were provided with red-painted sticks at 50 m intervals, with aluminium tags showing their coordinates in relation to an A axis directed NE and a B axis SE-ward with their origin at the western corner of the study area.

After trailcutting, a vegetation map was made by first locating in steps along all trails the vegetation boundaries and marking them on the map. After this, each vegetation boundary was followed by compass and mapped. Obviously, vegetation mapping is most accurate where the trail system is most extensive, namely in the main part of the spider monkey home range.

The forest in the study area can be divided into four major types (Fig. 6). High forest predominates, followed by liane forest and mountain savanna forest. Pina swamp forest grows along the small creeks that flow through the area. Low forest is present as a transitional type but hasn't been mapped, as it usually occurs in narrow strips along the borders of liane forest. The Voltzberg study area has a greater diversity of forest types and edge habitats than would usually be expected in a tract of similar size in the interior. Probably, this is caused by the abundant granite outcroppings that do not provide sufficient support for most tall forest trees, but do permit the growth of comparatively rare formations like mountain savanna forest and liane forest.

Because spider monkeys never enter low forest or liane forest, these formations, together with open granite, can act as natural boundaries. As shown in Fig. 6, large liane forest complexes and the Voltzberg itself do form for a considerable part the boundaries of the spider monkey home range, giving it a peninsula-like appearance.

Other animals present. All eight primate species were well represented. Besides *Ateles paniscus*, one could regularly observe *Saguinus midas*, *Saimiri sciureus*, *Cebus apella*, *Cebus nigrivittatus*, *Chiropotes satanas*, *Pithecia pithecia* and *Alouatta seniculus*. In addition to these primate species, a number of other mammals, birds and reptiles inhabit the Voltzberg study area as well. Larger rodents like the agouti (*Dasyprocta leporina*) and the acouchi (*Myoprocta exilis*) are common. Two species of squirrels (*Sciurillus pusillus*, *Sciurus aestuans*) and the prehensile-tailed porcupine (*Coendu prehensilis*) also occur, but are rarely seen. The carnivores are represented by one or two jaguars (*Panthera onca*), several ocelots (*Felis pardalis*) and tayra's (*Eira barbara*). Edentates include the giant armadillo (*Priodontes giganteus*), the nine-banded armadillo (*Dasypus novemcinctus*), the tamandua (*Tamandua longicaudata*), the giant anteater (*Myrmecophaga tridactyla*), and both species of sloths (*Choloepus didactylus*, *Bradypus tridactylus*). The common opossum (*Didelphis marsupialis*) and several smaller species (e.g., *Marmosa* spp.) are present. Ungulates are represented by several collared peccaries (*Tayassu tajacu*) and at least one tapir (*Tapirus terrestris*).

Many species of birds live in the study area and a complete list may be found in Mittermeier and Milton (1976) and the field checklist of the Birds of the Guiana's (Davis, 1966). The most conspicuous are large species

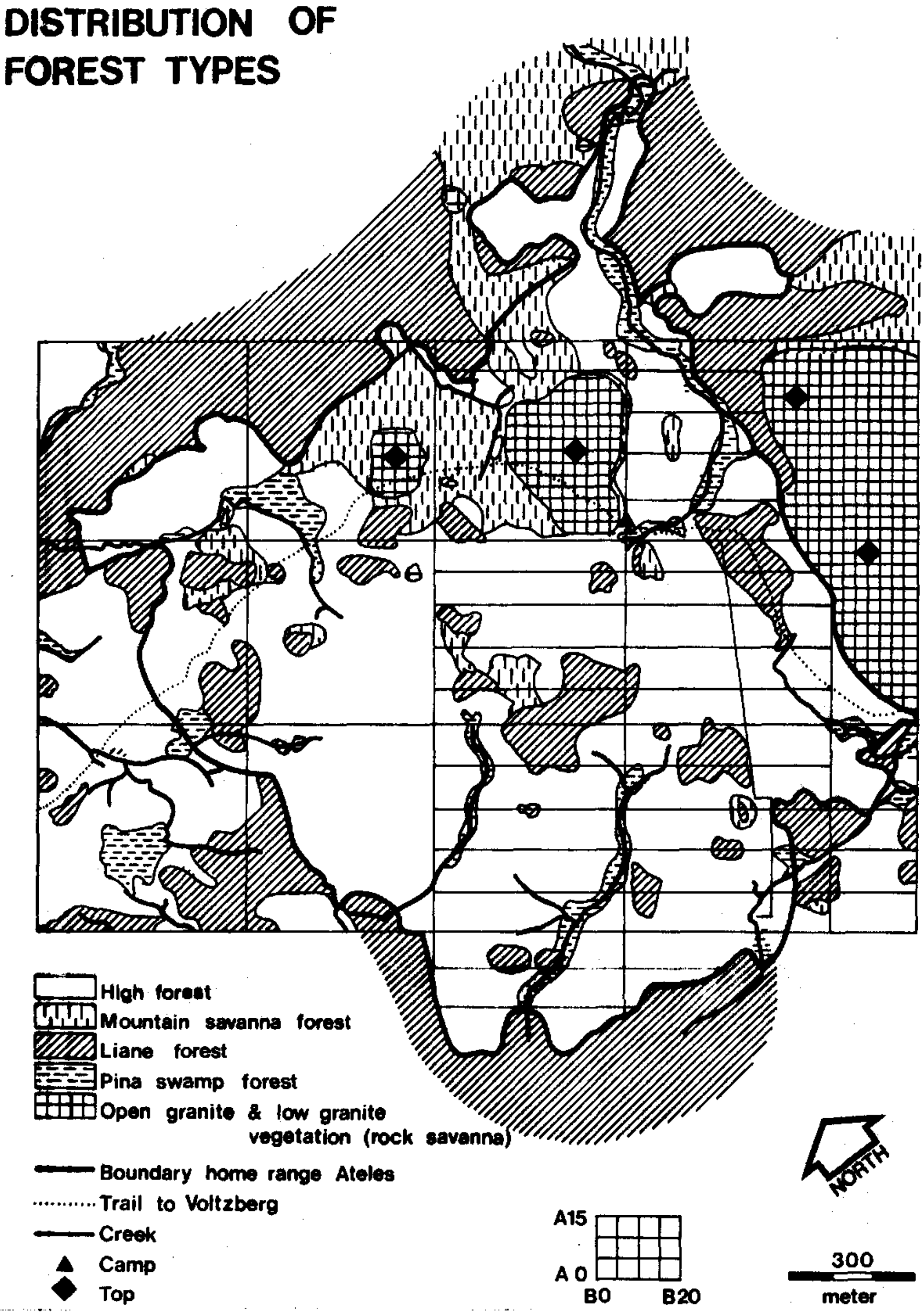


Fig. 6. Map of the Voltzberg study area showing distribution of forest types and trail system. The areas of open granite, low granite vegetation ('rock savanna') and liane forest were not used by the spider monkeys. The large area of open granite at the right is the Voltzberg dome with two tops. The camp is situated at the edge of the largest of both open granite plates. The perimeter of the spider-monkey group range is marked by a heavy line.

like the black curassow (*Crax alector*), the marail guan (*Penelope marail*), the gray-winged trumpeter (*Psophia crepitans*) and the tinamous (*Tinamus* spp.). Cocks-of-the-rock (*Rupicola rupicola*) are surprisingly abundant. An important lek area (display ground) and many nesting sites were found within and nearby the study area. In the canopy are scarlet macaws (*Ara macao*), toucans (*Rhamphastos* spp.), aracaris (*Pteroglossus* spp.) and a variety of parrots, esp. red fan parrots (*Deroptyus accipitrinus*), orange-winged parrots (*Amazona amazonica*) and mealy parrots (*Amazona farinosa*). A number of raptors, including the harpy eagle (*Harpia harpyja*), occasionally visit the study area as well.

Frogs, lizards and snakes are common, and the turtles are represented by two abundant forest tortoises (*Geochelone carbonaria* and *Geochelone denticulata*).

Insect life is varied and abundant, but mosquitos are rare. Discomfort usually is caused by chiggers and a number of stinging and biting ants.

2.2. *Data Collection*

2.2.1. *Habituation of spider monkeys*. During the first year, when the synecological part of the study took place, a group of spider monkeys was selected for detailed study on the autecology during the second year (May 1977 - May 1978). Thanks to the undisturbed condition of the area since tens of years or longer, the animals were not particularly shy. From time to time, a group of tourists was walking along the main trail to the Voltzberg through part of the group's range. It is likely that each member of the group saw people before this study started. Anyhow, all animals, except for a male, didn't react anymore upon people with their usual performance of shouting, shaking and dropping dead twigs and branches, and defecating like they do at first contact with human intruders. Also, they didn't flee away immediately at the first glimpse of a human being like spider monkeys tend to do in areas disturbed by hunting.

While studying mainly the synecology of the eight Surinam primate species during the first year, many census walks of the entire study area were made and also data were collected while looking for or tracking 'target' species. In this way, many contacts took place with all members of the study group of spider monkeys and occasionally with members of the two other groups that touched the study area. Everytime spider monkeys were located, data were collected for synecological purposes at first contact, and it was tried to follow them as long as possible. When obviously too excited by continued persecution, the observer stopped following and returned to the trail in search for other monkeys. Especially the cutting of palm leaves, saplings and lianes seemed to disturb the monkeys most, but after a while the observer got very experienced in zigzagging through the shrub layer without cutting much.

During February, March and April, 1977, it was tried to follow subgroups of spider monkeys as long as possible. After many attempts and helped by the observer's growing experience to walk freely through the forest while keeping visual, but particularly auditive contact, at the beginning of April, 1977, it was possible to track spider monkeys day after day without noticeably disturbing their ranging behaviour nor activity patterns anymore. Working alone seemed to be essential for this job. When accompanied by one or more others, it was hard to keep up contact and the monkey's behaviour seemed to be influenced significantly.

2.2.2. *The synecological part*. The synecology study in the Voltzberg study area was initiated in March, 1976. Till April, 1977, during 10 - 15 days each month, synecological data were gathered on all eight primate species. A total of 132 field days were spent studying synecology only.

During the first phase and later on, also my colleague R.A. Mittermeier collected data on synecology. These data were gathered by us during 12 census walks of the entire study area, spread over several months, and while looking for and tracking 'target' species selected for a given day. The following kinds of information were recorded every time a group was encountered: time, location in the study area, forest type, edge or non-edge habitat, activity (resting, travelling, feeding on plant food, foraging for or feeding on insects), height and level in the forest, how located (e.g., spontaneously seen, heard vocalizing, heard crashing, heard dropping fruit or faeces), path-animal distance, observer-animal distance (both for census purposes), group size and, if possible, group composition, and direction of travel. All data on preferences for different forest types, vertical stratification, activity and location of the group were based on first sightings only, in order to avoid possible bias caused by the presence of the observer. Usually, in particular with spider monkeys, the visible members of a (sub)group were at first sighting all engaged in the same activity at the same level and in the same forest type. In order to avoid confusion, first sighting data were based on the first individual actually seen, which is essentially an instantaneous focal animal sample.

A sighting was considered at an edge when the first animal seen was within 20 m of a clearing or another forest type. Feeding on plant food was considered the activity when the first animal was eating fruits, leaves, flowers or vegetable matter. Foraging for or feeding on insects was considered the activity when the first animal seen was eating or actively searching insects or other animal life.

For stratification observations, the forest was divided into six levels: shrub layer (0 - 3 m), understory (3 - 15 m), lower part of the canopy (15 - 20 m), middle part of the canopy (20 - 25 m), upper part of the canopy (25 - 30 m), and emergents (30 - 60 m).
Mostly, it was impossible to estimate the height of emergents accurately because of intervening vegetation and the limitations of the clinometer. However, it was usually quite easy to determine whether or not a tree was an emergent simply by its relationship to surrounding trees.

Location within the study area was determined by using the markers situated at 50 m intervals along the trails. Measuring the distance from a particular tree to the nearest marker in steps gave quite accurately the coordinates of the place.

Gathering synecological data as described above was continued during the second part of the study, on the autecology of the spider monkey, but because Ateles was the 'target' species, synecological data were only collected while in search of spider monkeys or when other species were encountered while tracking spider monkeys.

2.2.3. The autecological part. The study on the autecology of spider monkeys in a strict sense was started in the Voltzberg study area at the end of April, 1977, and lasted till the beginning of May, 1978. Each month of this full year, it was strived to get as much as seven full days of observation, but in several months only five or six days were realizable. A total of 135 field days were spent during this period, resulting in over 865 hours of observing spider monkeys only. For this purpose, each month usually 10 - 14 days had to be spent in the Voltzberg study area, divided in two sessions of 5 - 7 days each. As a rule, the first and the third week were spent in the Voltzberg study area, sometimes the second and the fourth week.

For spotting a 'target' subgroup of spider monkeys to start a session, several methods could be used. After an absence of 7 - 10 days, when arriving in the study area, every time the situation had drastically changed. Different fructifying plant species or individual plants usually resulted in completely different foraging routes of the monkeys. Every time a fresh start had to be made. Part of the trail system was covered till encountering a subgroup. This searching could last for hours or sometimes even a day. By performing a long call, occasionally as a response to an imitation call given by me, a male spider monkey could help in gaining time. Using a compass, finding this male or 'his' subgroup could succeed, or at least efforts could be concentrated to a certain area. In case of prolonged lack of success, the Voltzberg could be climbed in the late afternoon hoping to see spider monkeys entering one of their huge, usually leafless or early flushing sleeping trees. If so, the tree was located before returning to the camp and next day it was tried to be present at the foot of this tree at 5.45 h. Then, it was necessary to stick to them till the evening, between 17.00 - 18.30 h, when they entered another sleeping tree. In case of loosing contact, one had to return to the nearest trail and try to encounter this or another subgroup as soon as possible.

Because spider monkey subgroups join and split freely from time to time, it was hard to follow one focal animal all day long. For this purpose, it was preferred to follow a mother with offspring, who were easier to recognize at the confusing moment of a sudden fission. Still, as far as possible, an attempt was made to spread attention evenly over all members of the study group.

While tracking a subgroup of spider monkeys, the following data were collected. At five-minute intervals the composition of the subgroup was recorded, the activity of all members of the subgroup, and the stratum and forest type occupied. The coordinates of every crossing with trails were recorded by pacing the distance to the nearest pole (max. 50 m).

When feeding, complete samples (e.g., infructescences, inflorescences and/or leaves) were collected as far as possible. Usually, several visits of particular food plants were needed for this since, in general, spider monkeys used their food sources very economically. When it was not possible to collect a representative and complete sample dropped by the monkeys, the food plant was collected as soon as possible in cooperation with a native tree climber of 's Landsbosbeheer. Each food tree or liane, actually used by monkeys, was marked with a numbered aluminium tag together with a piece of red fluorescent plastic tape, by nailing the tag just after the monkeys left the tree. Using a water-resistant pencil, date and monkey species was written on the plastic tape and, after, the coordinates of the food plant were determined. Food samples were collected in plastic bags tightened by a piece of plastic tape on which time and tag number was written. Back in camp, a picture of all food items of a particular day was made using a Nikormat EL camera with 52 mm macrolens, and as soon as possible the samples were preserved by adding some formaldehyde (2% sol.). All samples were labelled. Back at the main base on Foengoe Island, all samples were identified if possible, using the book on the fruits of Surinam and some monographs of certain plant families and genera. After making a drawing of each new food item, including cross-sections and details, all samples were put in jars, labelled and administrated.

Also faeces were collected as good as possible and preserved. Faeces of spider monkeys usually contain mainly undigested and unharmed seeds and stones, in particular during the wet seasons. Consequently, the faeces were not compact at all and usually dispersed over quite a big area. Depending on the available time, as much seeds and/or stones as possible were collected from the forest floor. By collecting and naming all fruits found on the forest floor in a particular period, mostly also seeds and stones of fruit species, that didn't yet occur on the diet list, could be identified from faeces.

In September, 1977, together with the native tree specialist and an assistant, a marking program was initiated lasting about seven months. By then, almost all important food species were determined, many of them already collected during the synecological part of the study. A list of 120 important species was compiled, including food trees, easily recognizable lianes and some sleeping trees, using vernacular names. When a species was new to the tree specialist, several individuals were shown to him in order to learn its special properties like type of habit, colour, taste and texture of bark and/or wood, presence of latex, type of leaves if visible, etc. Each species was given a code number. The most important part of the home range of the study group, approx. 205 ha, was inventoried. For this purpose, new transects were cut at 50 m intervals, perpendicular to the 100 m trails, resulting in about 370 rectangular blocks, a ½ ha each (Appendix). All individual trees and lianes belonging to the listed species were marked with a numbered aluminium tag differing from the above mentioned ones that were used when spider monkeys actually were seen feeding on it. In this way, block after block was inventoried and the location of a numbered plant was determined approximately by its place in a certain ½ ha block. Trees below 12 m were not included because this was determined the lower limit of the vertical range of spider monkeys. For the purposes of this study, tagging and plotting was restricted to those individual plants, that obviously had reached 'their' preferred stratum which, in general, implies the phenomenon of flowering and fruiting. Plants providing the monkeys only with edible flush leaves were plotted when reaching 12 m or more whether they had reached 'their' stratum or not.

A total of about 10.000 trees and lianes were marked and plotted in special maps in order to determine their density and pattern of distribution. In this way most of the trees and lianes, marked when seen spider monkeys feeding on it, were marked again, giving a double check of its identification and location. Also, it gave an idea of the reliability of the tree specialist, which turned out to be excellent.

For measurement of diet composition, the frequency was used with which different foods were chosen. If a subgroup or a solitary ranging animal was seen feeding on a single food plant, one observation was scored. If a subgroup or individual moved to another tree of the same species, another observation was scored. If a subgroup or individual moved to a different food plant species, one observation was scored for that species. If identifiable seeds or stones of a given species, not seen eaten before during that day, were found in the faeces of a single monkey, one observation was scored for that species. This method may seem to be somewhat crude, but it worked out to give a good estimate of the relative importance of different food plant species and families in spider monkey diet. It is preferred above determining the total feeding time for each species, because feeding rate can vary widely between foods. Some fruits are swallowed whole, others are woody and indehiscent and have to be opened first. Some fruits contain a lot of nutritive pulp and comparatively small seeds or stones, others, for instance, produce very little pulp or are eaten only for a minuscule aril.

Measurement of the proportion of feeding time spent on different foods has also the disadvantage that analysis of dung samples cannot be taken into account. Particularly in spider monkeys dung samples can give a lot of information since the animals swallow indigestible seeds and stones in 93.5% of all fruit feeding observations.

The chosen method produces some bias towards foods that are eaten regularly but in small amounts, and towards plant species that produce several edible items at the same time. Both features, however, are rare in the case of spider monkeys and consequently the bias is of little importance. A relatively more important bias may be produced towards species that grow in clumps and widely dispersed ones. For instance, Virola melinonii (Myristicaceae) can be overestimated in this method because it tends to grow in clumps. When feeding on a particular tree of this species, the monkeys will visit one or more trees nearby too, that provide only small food supplies and consequently should have been neglected when they had to spend more energy and time to reach it.

2.3. The General Survey

Some other localities were investigated during the general survey, adding data for the distribution map and the habitat table of Ateles.

2.3.1. Lolopasi, west bank Coppename River, Raleighvallen-Voltzberg Nature Reserve. Lolopasi is located directly across the Coppename River from Foengoe Island, site of the headquarters of Raleighvallen-Voltzberg Nature Reserve. A trail of 2.9 km has been cut through the forest to enable visitors to reach the Moedervallen, largest of the Raleighvallen rapids. During the first part of the study, additional trails were cut to the west about perpendicular to the riverbank 600 - 1000 m inland, at 500 m intervals (Fig. 5). The trail system was not finished. In total 7 km came available.

The Lolopasi area consists almost entirely of riverbank high forest and high forest, except for a narrow strip of marsh forest close to the bank of the Coppename. Pina swamp forest and some liane forest are present, but no mountain savanna forest was encountered.

All eight Surinam monkey species occurred in the area, but some of the species, in particular Ateles, were very shy because of recent hunting. It was impossible to follow spider monkeys for longer than half an hour. No progress could be made in the habituation of the monkeys. A rough idea of the population and the diet could be determined.

2.3.2. Kayser Mountains. The Kayser Mountains are located in the interior in southwest Surinam. The Surinam Geological Service carried out survey work and opened a big area by cutting transects. A two-week survey was carried out here in September, 1976, using their trail system of about 40 km for census walks. The area was fully undisturbed except for occasional hunting by the workers. Because of high densities of certain game species like black curassows (Crax alector) and peccaries (Tayassu tajacu and Dicotyles pecari), these people didn't hunt for monkeys. The spider monkeys were not at all shy and reacted like they use to do at first contact with human intruders. The density of spider monkeys and several other monkey species seemed to be somewhat higher than in the Voltzberg area. Food scarcity in the long dry season seemed to be less severe.

The vegetation is primarily high forest and mountain savanna forest, with some pina swamp forest in low-lying areas. Above 400 m, the boegroemaka palm (Astrocaryum sciophilum) in the undergrowth and shrub layer of high forest is replaced by the bergimaripa palm (Attalea speciosa), here reaching the canopy (15 - 18 m).

Additional data on diet, subgroup composition and habitat preferences of Ateles paniscus were collected besides synecological data on all monkey species.

2.3.3. Other parts of Surinam. Locality data for the distribution map (Fig. 1) were taken from museum specimens of Surinam monkeys, from field observations of R.A. Mittermeier and from observations reported personally by several other naturalists well-acquainted with the monkeys.

3. HABITAT PREFERENCES

3.1. Preferences for Different Forest Types

Where little or no hunting has taken place, Ateles p. paniscus can be

quite abundant in tracts of high forest. It also occurs in riverbank high forest but in this habitat often severe hunting by Bushnegroes and/or Amerindians has taken place or, in uninhabited areas at least some hunting has taken place in recent past by occasional visitors like workers of Meteorological, Geological and/or Mining Services. I never observed spider monkeys right at the river front. The reasons may be unpleasant hunting experience in the past, tendency of the monkey to avoid edge habitats and/or lack of edible food plant species at the river margins.
Ateles was seen in Surinam once in marsh forest, once in high savanna forest growing on the Coesewijne formation and three times in Eperua falcata savanna forest (Mittermeier, 1977).

Ateles spp. also apparently prefer undisturbed high forest in other parts of South America (e.g., Janson, 1975; Bernstein, et al., 1976; Hernández-Camacho and Cooper, 1976). Usually, it is not found in areas where human activity has resulted in forest destruction. The absence in most areas with human activity may result from the hunting pressure frequently accompanying partial habitat destruction, rather than the monkey's inability to survive in isolated patches of habitat.
Ateles geoffroyi of Central America is apparently more flexible in choice of habitat than most of its South American relatives. Freese (1976) observed A. geoffroyi in evergreen, semi-deciduous and sometimes even deciduous forest in Costa Rica, and Eisenberg and Kuehn (1966) and Alvarez del Toro (1977) report it from mangrove forest in Chiapas, Mexico.
The available evidence indicates that Ateles prefers undisturbed high forest, but where such habitat is limited in extent, and where hunting pressure is light or non-existent and other primate competitors are few in number, it appears to be able to live in several other forest types as well.

In the Voltzberg region Ateles is predominantly seen in high rain forest (Fig. 7A). Of all first sightings 92.6% occurred in high forest. Only occasionally, it entered high mountain forest (4.4%), particularly when some species typical for this vegetation type were fruiting. During the long dry season mountain savanna forest has almost nothing to offer for spider monkeys, and consequently they were seen there very rarely at this time of year.
The third forest type, where Ateles was occasionally seen, is pina swamp forest (3.0%). It didn't avoid this type of forest while travelling, using the flexible stems of the pina palms (Euterpe oleracea) as jumping-poles while hanging in its small crowns. There are some tree species typical for pina swamp forest, like Eperua falcata, Carapa procera, Pterocarpus officinalis, Virola surinamensis and Euterpe oleracea itself, that offer edible fruit, leaves and/or flowers and make them visit it more often during part of the year.
I never observed Ateles in the other available habitats in the Voltzberg region (e.g., liane forest, low forest and 'rocksavanna'). In the Lolopasi area, Ateles was seen many times in riverbank high forest, but never within 150 m from the riverbank itself. However, its home range was situated with its long axis perpendicular to the riverbank and its centre beyond the boundary-line between riverbank high forest and high forest, at about 700 m inland. Whether this situation was original or influenced by light hunting pressure was not clear.

Of all Surinam monkey species Ateles paniscus is the most restricted in habitat (Mittermeier and Van Roosmalen, in press). Only the bearded saki (Chiropotes satanas) shows a somewhat similar restriction in habitat choice. All other Surinam monkey species visit more or less frequently liane forest and/or low forest.

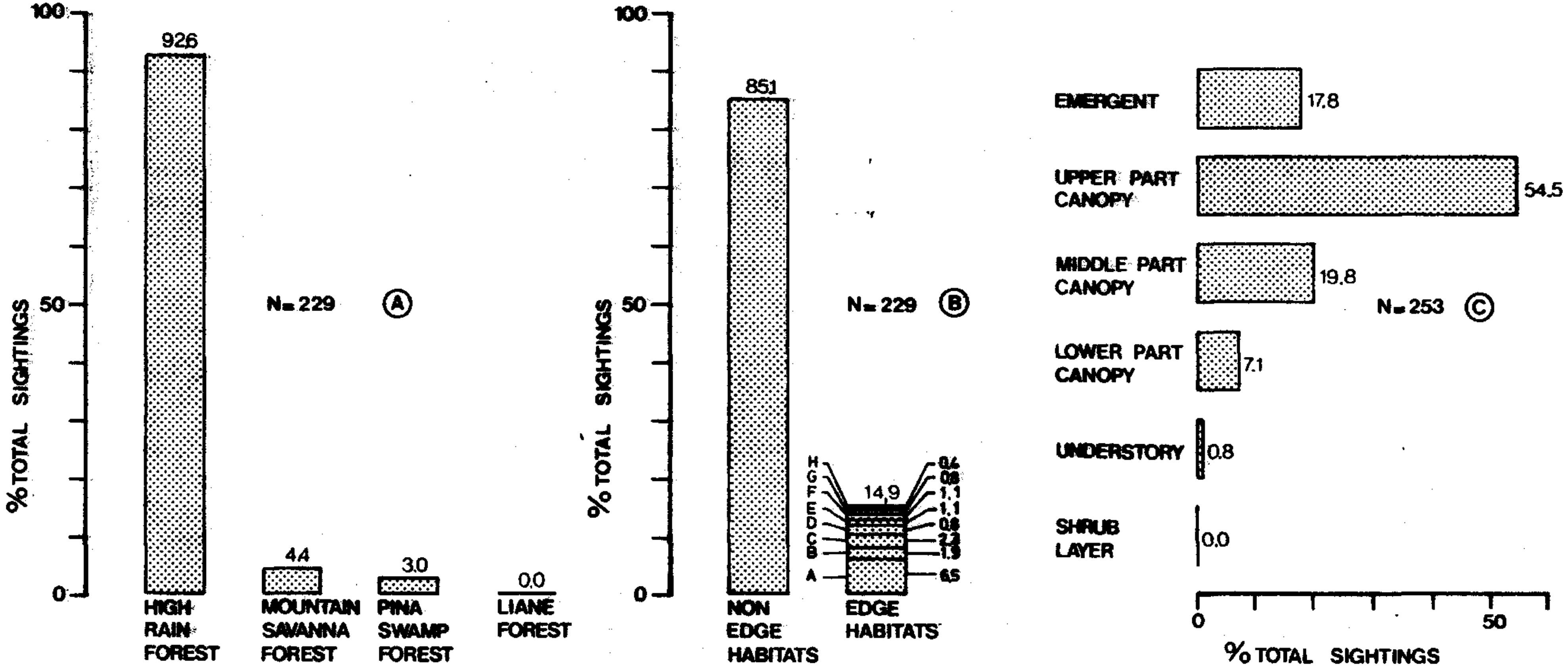


Fig. 7. Habitat preferences of Ateles p. paniscus in the Voltzberg study area. Data are based on first sightings only.

A. Forest Type Preferences

B. Utilization of Edge Habitats (A = high forest/edge pina swamp forest; B = high forest/edge liane forest; C = high forest/edge clearing; D = high forest/edge mountain savanna forest; E = pina swamp forest/edge high forest; F = mountain savanna forest/edge clearing; G = mountain savanna forest/edge liane forest; H = mountain savanna forest/edge high forest)

C. Utilization of forest strata.

3.2. Edge Preferences

At the Voltzberg study site, an area rich in edge habitats, *Ateles* didn't show any preference for those areas (Fig. 7B). In 85.1% of *total first* sightings, it was seen in non-edge habitats. In 14.9% it was seen in edge habitats, of which only 6.1% in edges with clearings or liane forest. Where hunting didn't take place in the recent past, spider monkeys not at all seemed to be afraid to expose themselves at edges of open areas. Several of the sleeping trees, strongly selected in a certain time of the year, were situated at the very edge of clearings and/or liane forest. The only reason why they appear to avoid edge habitats is that these habitats do not offer them special food sources like they do for partly insectivorous species.

Of the eight Surinam monkey species, only *Saguinus midas* was seen more often in edge habitats than in non-edge habitats (Mittermeier and Van Roosmalen, in press). Also *Saimiri sciureus* and *Cebus apella* are apparently partial to edge habitats. They tend to follow the edges of liane forest complexes in search of insects. *Alouatta seniculus* and *Pithecia pithecia* occurred somewhat more often in edge habitats than *Ateles* did, and *Chiropotes satanas* and *Cebus nigrivittatus* less often.

3.3. Vertical Stratification

Ateles is primarily an animal of the upper levels of the forest with 17.8% of first sightings in emergents and 54.5% in the upper part of the canopy. The middle levels of the forest were less frequently used, with 19.8% of first sightings in the middle part of the canopy and only 7.1% in the lower part of the canopy. *Ateles* very rarely entered the understory and was seen there only in 0.8% of first sightings (Fig. 7C).

Of the other Surinam monkey species only *Chiropotes satanas* shows a vertical distribution very similar to that of *Ateles*, with 63.0% of first sightings (n=27) in the two uppermost strata. All other Surinam monkey species prefer the middle and/or lower strata (Mittermeier and Van Roosmalen, in press).

In general, *Ateles* is the most restricted species in the Voltzberg area. It occurs almost exclusively in high forest, infrequently enters edges and has the lowest values for overall forest type niche breadth (Mittermeier and Van Roosmalen, in press). It occurs primarily in the upper levels of the canopy and in emergents, and has the second lowest vertical stratification niche breadth value.

4. DIET

4.1. Food Categories

In this study, spider monkey food was categorized as (1) *fruits* - including young seeds, mature seeds, stones, plumula, aril, exocarp, mesocarp, endocarp, pericarp, perigonium, infructescence, compound fruit, fig, pseudofruit, juice and columella, (2) *flowers* - including floral buds, mature flowers and inflorescences, (3) *leaves* - including leaf buds, young or flush leaves, mature leaves, petiole and tender shoot, (4) *bark*, (5) *decaying wood*, (6) *pseudobulbs*, (7) *aerial roots*, (8) *honey* and (9) *insects*.

In Table 1, among other things, all food species and the part(s) eaten are listed, ordered alphabetically first to family, then to genus and last to species. In total, 207 food plant species were recognized, of which 68.1% were trees, 25.6% lianes and stranglers, 1% herbaceous twiners and 5.3% epiphytes (Table 2).

Of the 58 plant families used by the spider monkeys, *Moraceae* were the best represented with 29 species, followed by *Mimosaceae* (18 species),

TABLE: 1. FOOD LIST OF ATELES PANISCUS IN SURINAM

List of signs and abbreviations:

- not observed in Voltzberg study area, sp. = species, infruct. = infructescences, inflor. = inflorescences x = dispersal and/or predation,
— = nil, — max. height in meters, h. riverb. f. = high riverbank forest, h. mount. sav. f. = high mountain savanna forest, rocksav. = rocksavanna,
l. mount. sav. f. = low mountain savanna forest, sec. f. = secondary forest, pl. = places, esp. = especially, ✱ = number of food plants used by the study group, () = not occurring in Voltzberg study area, o = mature fruit, y = young seeds, f = flowers, b = bark, m = miscellaneous,
l = young leaves

FAMILY / Species	parts eaten	seed dispersal	seed predation	habit of plant	forest type	no. of food plants	no./km^2	fruiting/flowering period(s)/time(s) of availability											
								J	F	M	A	M	J	J	A	S	O	N	D
ANACARDIACEAE																			
Anacardium giganteum Hancock	pseudofruit (= pedicel)	-	-	tree — 30m	h.forest + h.riverb.f.	23	11		o o	o									
Spondias mombin L.	mesocarp	x		tree — 30m	h.mount.sav.f. + creekf. on swampy places	28	13				o o	o o	o						
ANNONACEAE																			
Duguetia sp. (new species)	infruct.	x		tree — 15m	h.mount.sav.f.	14	7			o	o o	o							
Ephedranthus guianensis R.E.Fr.	mesocarp	x		tree — 15m	high forest	312	149	o	o				o o	o					
Guatteria chrysopetala (Steud.) Miq.	whole fruit	x		tree — 25m	high forest	1	0,5										o	o o	o
Malmea obovata R.E.Fr.	whole fruit	x		tree — 12m	high forest	-	-	o o				o	o o	o					
Unonopsis glaucopetala R.E.Fr.	whole fruit	x		tree — 20m	high forest	63	30										o	o o	o
APOCYNACEAE																			
Geissospermum sp.	juice	-	-	tree — 30m	high forest	7	3			o	o o								
Parahancornia amapa (Hub.) Ducke	mesocarp	x		tree — 40m	high forest + h.riverb.f.	-	-			o o									
ARACEAE																			
Monstera adansonii (Schott) Madison	infruct.	x		epiphyte 'rootclimber'	high forest + h.mount.sav.f.	-	-					o o							
Philodendron acutatum Schott	infruct. young leaves tips of aerial roots	x		epiphyte	high forest	common		o o			1 1 m m			1	1 1	o o 1 1	o o 1 1	o o 1 1	o o 1 m m
Philodendron scandens C.Koch et Sello	infruct. young leaves + base of petiole tips of aerial roots	x		lianalike epiphyte 'rootclimber'	high forest	common		1 1	1 1	1 1	1 1	1 1	1 1	o o 1 1 m m	1 1	1 1	1 1	1 1	1 1
Philodendron sp.	infruct. young leaves	x		epiphyte	high forest	-	-								o o	1 1	o	o o	o o

FAMILY / Species	parts eaten	seed dispersal	seed predation	habit of plant	forest type	no. of food plants	no./km^2	fruiting/flowering period(s)/time(s) of availability											
								J	F	M	A	M	J	J	A	S	O	N	D
BIGNONIACEAE																			
Stizophyllum inaequilaterum Bur.et K.Schum.	flowers	-	-	liana	high forest	-	-											f f	
Tanaecium jaroba Sw.	young seeds		x	liana	high forest	-	-	y y	y y	y									
Tabebuia capitata (Bur.et K.Schum.) Sandw.	flowers	-	-	tree — 35m	h.mount.sav.f.	15	7											f f	
Tabebuia serratifolia (Vahl)Nicholson	flowers young leaves	-	-	tree — 35m	high forest + h.mount.sav.f. esp.swampy pl.	38	18	1 1								f f	f 1	1 1	1 1
Species a.	flowers	-	-	liana	high forest	-	-							f					
Species b.	flowers	-	-	liana	high forest	-	-							f					
Adenocalymna sp.	flowers	-	-	liana	h.f.+h.m.s.+ h.r.b.f.	-	-									f	f		
Arrabidaea corallina (Jacq.) Sandw.	flowers	-	-	liana	h.m.s.f.edges + rocksav.	-	-									f	f f		
Xylophragma seemannianum (O.Kuntze) Sandw.	flowers	-	-	liana	h.m.s.f. esp.at edges + h.r.b.f.	-	-											f f	f
Species c.	flowers	-	-	liana	high forest	-	-				f								
Bistrictella magnoliifolia (H.B.K.) Sandw.	flowers	-	-	liana	high forest	-	-											f	
Dystictis vs. granulosa	young leaves flowers young seeds		 x	liana	h.mount.sav.f.	-	-										1 1 f	1 1 y	1 y
BOMBACACEAE																			
Bombax spectabile Ulbrich	young leaves floral buds + flowers young seeds		 x	tree — 35m	high forest + pinaswamp	51	24		f	f f	f f y		f	1 f f	1 1 f	1 1	1 1		
Ceiba pentandra Gaertn.	floral buds + flowers young leaves exocarp of young fruits	-	-	tree — 50m	high forest + h.mount.sav.f. on swampy places	18	9											f f 1 1 o	 1 o
BORAGINACEAE																			
Cordia lomatoloba Johnston	mesocarp	x		tree — 25m	high forest	28	13	o	o o										
Cordia panicularis Rudge	whole fruit	x		tree — 20m	high forest								o o						
Cordia sagotii Johnston	whole fruit	x		tree — 20m	high forest, esp.at edges													o o	o

F A M I L Y / Species	parts eaten	seed dispersal	seed predation	habit of plant	forest type	no. of food plants	no./km^2	J	F	M	A	M	J	J	A	S	O	N	D
BURSERACEAE																			
Protium neglectum Swart	*mesocarp*	x		tree — 20m	high forest	311	148				o o	o							
Protium polybotryum (Turcz.) Engl.	mesocarp	x		tree — 25m	high forest	217	103				o o	o o							
Tetragastris altissima (Aubl.) Swart	mesocarp	x		tree — 30m	high forest	1631	777			o	o o	o o	o o						
Tetragastris panamensis (Engl.)O.Kuntze	mesocarp	x		tree — 25m	high forest	280	133				o o	o o	o o						
CACTACEAE																			
Hylocereus sp. a.	flowers whole fruit	 x		epiphyte	high forest + h.mount.sav.f. esp.at edges	-	-	f f	f f	f f o	f f	f f				f f	f f	f f	f f
Hylocereus sp. b.	whole fruit flowers	x		epiphyte	high forest + h.mount.sav.f. esp.at edges	-	-		o o	o o						 f f	 f f		
Pereskia aculeata Mill.	flowers whole fruit	 x		liana	h.mount.sav.f. esp.at edges	-	-	 o	 o o	 o								f	f
CAPPARACEAE																			
Capparis maroniensis R. Ben.	mesocarp	x		tree — 30m	high forest	304	145	o o	o o	o o	o o	o							
CARICACEAE																			
Jacaratia spinosa (Aubl.) A.DC.	whole fruit young leaves	x		tree — 20m	high forest + h.mount.sav.f. esp.at edges	7	3	 1 1				o o							
CELASTRACEAE																			
Cheiloclinium cognatum (Miers) A.C. Smith	(young)seeds		x	tree — 12m	high forest	20	10				y	y y							
Cheiloclinium cf.gleasonianum A.C. Smith	mesocarp	x		liana	h.riverb.f.	0	0			(o o	o o)								
Cheiloclinium podostemum (Sandw.) A.C. Smith	mesocarp	x		liana	high forest + h.riverb.f.	-	-					o o							
Cheiloclinium sp. (3549)	mesocarp	x		liana	high forest	1*	0,5*				o	o							
Cheiloclinium sp. (249)	mesocarp	x		liana	high forest	2*	1*			o o			o o						
Maytenus sp.	aril	x		tree — 30m	high forest + h.mount.sav.f.	3	1			o o		o o							
CHRYSOBALANACEAE																			
Couepia caryophylloides R. Ben.	exocarp + mesocarp	-	-	tree — 25m	high forest	99	47											o o	o
Licania densiflora Kleinh.	exocarp + mesocarp	-	-	tree — 30m	high forest	-	-				o o								
Licania majuscula ~~Sagot~~	exocarp + ~~mesocarp~~ bark	-	-	tree — 30m	high forest + h.mount.sav.f.	67	32	o o	o o	o o	o							o b b	o
Licania micrantha Miq.	young leaves bark	-	-	tree — 30m	high forest	49	23	 b b	 b b					 b				1 1 b b	 b b
Parinari campestris Aubl.	exocarp + mesocarp	-	-	tree — 25m	high forest + h.riverb.f.	12	6			o o	o o								
Parinari excelsa Sabine	exocarp + mesocarp	-	-	tree — 40m	high forest	22	10			o o						o o	o		

F A M I L Y / Species	parts eaten	seed dispersal	seed predation	habit of plant	forest type	no. of food plants	no./km²	fruiting/flowering period(s)/time(s) of availability J	F	M	A	M	J	J	A	S	O	N	D
COMBRETACEAE																			
Combretum rotundifolium L.C. Rich.	young seed		x	liana	high forest	common		y y											
CONVOLVULACEAE																			
Dicranostyles guianensis A. Mennega	mesocarp	x		liana	high forest	4*	2*					o o	o						
Maripa glabra Choisy	young seed		x	liana	high forest	-	-						y y						
Maripa scandens Aubl.	young seed		x	liana	high forest, esp.at edges	4	2					y y	y						
Operculina alata (Hamilt.) Urb.	young seeds		x	liana	at edges of h.mount.sav.f.	-	-											y	
CUCURBITACEAE																			
Cayaponia ophthalmica R.E. Schultes	mesocarp	x		liana	high forest, h.mount.sav.f. + h.riverb.f.	common			o	o o	o o	o							
Cayaponia rigida (Cogn.) Cogn.	whole fruit	x		liana	high forest	-	-				o o	o							
DIOSCOREACEAE																			
Dioscorea trifida?	young leaves	-	-	twiner	l.mount.sav.f. + edge rocksav.	-	-							l					
EUPHORBIACEAE																			
Alchorneopsis floribunda (Benth.) Muell.Arg.	whole fruit		x	tree — 30m	high forest + pinaswamp	2	1		y	y y									
Drypetes variabilis Uitt.	whole fruit	x		tree — 30m	high forest	35	17	o o	o o	o o	o								
Hyeronima laxiflora (Tul.) Muell.Arg.	whole fruit bark	x		tree — 30m	high forest	36	17	o	o	o o						o o		b b	
FLACOURTIACEAE																			
Laetia procera (P.et E.) Eichl.	aril	x		tree — 40m	high forest	30	14	o	o o	o o	o								
GESNERIACEAE																			
not identified species	young leaves	-	-	twiner	edges of h.mount.sav.f.	-	-												l
GNETACEAE																			
Gnetum urens (Aubl.) Blume	perigonium + seed(?)	x	x?	liana	high forest + h.riverb.f.	2	1	o o										o o	o o
GOUPIACEAE																			
Goupia glabra Aubl.	whole fruit	x		tree — 40m	high forest	8	4										o	o	
GUTTIFERAE/CLUSIACEAE																			
Clusia grandiflora Splitg.	aril	x		epiphytic liana(strangler)	high forest	-	-	o	o		o	o							
Clusia platystigma Eyma	♂ flowers, central body of staminodes	-	-	epiphytic liana	high forest	-	-									f f			

FAMILY / Species	parts eaten	seed dispersal	seed predation	habit of plant	forest type	no. of food plants	no./km^2	J	F	M	A	M	J	J	A	S	O	N	D
Clusia purpurea (Splitg.) Engl.	aril	x		epiphytic liana	high forest	-	-									o o			
Clusia scrobiculata R. Ben.	aril	x		epiphytic liana(strangler)	high forest	common			o o	o o	o o								
Clusia sp.	floral buds	-	-	epiphytic liana	high forest	-	-							f	f				
Platonia insignis Mart.	aril	x		tree — 35m	h.riverb.f.	2	1		.	o o	o o								
Rheedia benthamiana Tr.et Pl.	aril	x		tree — 15m	high forest	7	3									o o			
Rheedia macrophylla (Mart.) Tr.et Pl.	aril	x		tree — 20m	high forest	88	42				o	o o	o o						
Symphonia globulifera L.f.	flowers	-	-	tree — 25m	high forest + pinaswamp	2	1								f	f f			
HUMIRIACEAE																			
Sacoglottis cydonioides Cuatr.	whole fruit bark	x		tree — 30m	high forest	21	10	o o	o o	o o b		o	o					b	b
ICACINACEAE																			
Leretia cordata Vell.	whole fruit	x		liana	high forest	-	-							o	o o	o			
Leretia sp.	exocarp + mesocarp	-	-	liana	high forest	-	-												o
LAURACEAE																			
Licaria canella (Meissn.) Kosterm.	young leaves	-	-	tree — 25m	h.mount.sav.f.	2	1											l	l
Nectandra cf. kunthiana (Nees) Kosterm.	bark	-	-	tree — 30m	h.mount.sav.f.	24	11											b	
Ocotea wachenheimii R. Ben.	whole fruit	x		tree — 28m	high forest	2	1			o o									
LECYTHIDACEAE																			
Couratari guianensis Aubl.	young seeds		x	tree — 50m	high forest + h.riverb.f.	17	8			y y									
Couratari stellata A.C. Smith	young seeds bark		x	tree — 45m	high forest	403	29					y y	y y						b
Eschweilera congestiflora (R.Ben.) Eyma	young seeds + aril		x	tree — 25m	high forest	2	1	y y	y										y y
Eschweilera corrugata (Poit.) Miers	young seeds + aril		x	tree — 25m	high forest + pinaswamp	761	362	y y	y y	y y	y y								
Eschweilera poiteaui (Berg) Ndz.	young seeds + aril		x	tree — 35m	high forest	336	160				y	y y							
Gustavia hexapetala (Aubl.) J.E. Smith	mesocarp + funicle	x		tree — 15m	high forest + h.mount.sav.f.	-	-										o o	o	
Lecythis davisii Sandw.	mesocarp	-	-	tree — 30m	high forest + h.riverb.f.	0	0								(o o)				

FAMILY / Species	parts eaten	seed dispersal	seed predation	habit of plant	forest type	no. of food plants	no./km^2	fruiting/flowering period(s)/time(s) of availability											
								J	F	M	A	M	J	J	A	S	O	N	D
LEGUMINOSAE/CAESALPINIACEAE																			
Copaifera epunctata Amsh.	aril	x		tree — 40m	high forest	0	0									(o o	o)		
Copaifera guianensis Desf.	aril	x		tree — 40m	high forest + h.riverb.f.	14	7	o o											
Cynometra marginata Benth.	young leaves	-	-	tree — 20m	high forest, esp.on swampy places	-	-				1 1								
Dialium guianense (Aubl.) Steud.	aril	x		tree — 30m	h.mount.sav.f.	13	6					o o	o o	o o	o o	o			
Dimorphandra multiflora Ducke	mesocarp bark	x		tree — 45m	high forest	35	17						o o	o o	o o	o o	o o	o o b b	o o
Eperua falcata Aubl.	plumula flowers young leaves		x	tree — 30m	high forest + pinaswamp	102	49	f f 1	1		y	y y						f f	f f
Eperua rubiginosa Miq.	plumula		x	tree — 30m	h.riverb.f. + creekforest	1	0,5	(y y)											
Peltogyne venosa (Vahl) Benth.	aril	x		tree — 35m	high forest, esp.along creeks	0	0									(o o)			
LEGUMINOSAE/MIMOSACEAE																			
Cedrelinga cateniformis (Ducke) Ducke	young seeds		x	tree — 60m	high forest	34	16	y y											y
Enterolobium schomburgkii Benth.	inflor.	-	-	tree — 40m	high forest	12	6	f	f										
Inga acreana Harms	mesocarp	x		tree — 25m	high forest	96	46			o	o o	o o	o						
Inga acrocephala Steud.	mesocarp	x		tree — 20m	high forest, esp.at edges	4*	2*	o	o o	o o									
Inga alba (Sw.) Willd.	mesocarp bark	x		tree — 35m	high forest	224	107	o o b b	o o b b	o o b b	b b							b	o b b
Inga bourgoni (Aubl.) DC.	mesocarp	x		tree — 20m	high forest, esp.at edges	11*	5*			o	o o	o							
Inga cf. capitata Desv.	mesocarp	x		tree — 20m	high forest	41	20				o o	o o	o						
Inga coriacea (Pers.) Desv.	mesocarp	x		tree — 25m	high forest	-	-						o o						
Inga edulis Mart.	mesocarp	x		tree — 30m	high forest, esp.at edges + sec.forest	20*	10*		o	o o	o o								
Inga leiocalycina Benth.	mesocarp bark	x		tree — 25m	high forest, esp.along creeks	6*	3*			o o	o							b	b
Inga pezizifera Benth.	mesocarp	x		tree — 25m	high forest	-	-					o o							
Inga rubiginosa (L.C.Rich.) DC.	mesocarp	x		tree — 25m	high forest	-	-			o o									
Inga stipularis DC.	mesocarp	x		tree — 25m	high forest + pina swamp	-	-				o o								
Inga thibaudiana DC.	mesocarp	x		tree — 25m	high forest esp.at edges	-	-	o o											

F A M I L Y / Species	parts eaten	seed dispersal	seed predation	habit of plant	forest type	no. of food plants	no./km^2	J	F	M	A	M	J	J	A	S	O	N	D
<u>Newtonia suaveolens</u> (Miq.) Brenan	inflor. (young buds)	-	-	tree — 50m	high forest	45	21	f	f										
<u>Parkia nitida</u> Miq.	inflor. mesocarp	 x		tree — 50m	high forest	11	5					f	f f	f			 o	 o	
<u>Parkia pendula</u> (Willd.) Benth.	inflor.	-	-	tree — 45m	high forest	15	7								f	f			
<u>Pithecellobium jupunba</u> (Willd.) Urb.	young leaves bark	-	-	tree — 35m	high forest	36	17							l				 b	
LEGUMINOSAE/PAPILIONACEAE																			
<u>Dioclea macrocarpa</u> Huber	young seeds		x	liana	high forest	-	-	y											
<u>Dipteryx odorata</u> (Aubl.) Willd.	young leaves	-	-	tree — 30m	high forest	11	5					l					l		
<u>Hymenolobium petraeum</u> Ducke	young leaves	-	-	tree — 50m	high forest	8	4	l l											
<u>Ormosia paraensis</u> Ducke	young seeds		x	tree — 30m	high forest, esp. along creeks	0	0									(y)			
<u>Platymiscium ulei</u> Harms	flowers	-	-	tree — 30m	high forest	22	10									f f			
<u>Pterocarpus officinalis</u> Jacq. (+ P. vs. santalinoides)	young leaves	-	-	tree — 30m	pinaswamp + h.mount.sav.f.	110	52									l l	l l	l	
<u>Vataireopsis speciosa</u> Ducke	young leaves	-	-	tree — 45m	high forest	70	33	l l	l								l	l l	l l
LOGANIACEAE																			
<u>Strychnos tomentosa</u> Benth.	mesocarp	x		liana	high forest	3	1	o o	o o	o o	o o			o	o o	o o	o o		
LORANTHACEAE																			
<u>not identified species</u>	young fleshy leaves	-	-	epiphyte/ parasite	high forest	-	-										l l		
MARCGRAVIACEAE																			
<u>Norantea guianensis</u> Aubl.	flowers	-	-	liana	high forest, h.mount.sav.f., h.riverb.f.	8	4	f f	f f										f f
MELASTOMATACEAE																			
<u>Bellucia grossularioides</u> (L.) Triana	whole fruit	x		tree — 20m	h.mount.sav.f. on granite	2*	1*	o			o o							o o	o o
MELIACEAE																			
<u>Carapa procera</u> A.DC.	flowers young seeds young leaves		x	tree — 30m	high forest on swampy places + pinaswamp	417	199	f f y y l				 y y		 l	 l l	 l l	 l l	f f l	f f
<u>Cedrela odorata</u> L.	young seeds + columella		x	tree — 40m	high forest	9	4	y y											y y
<u>Guarea grandifolia</u> C.DC.	flowers aril	 x		tree — 30m	high forest	449	214				f f o o	 o o	 o o			f	f f o	f f o	
<u>Guarea kunthiana</u> A. Juss.	aril	x		tree — 30m	high forest + h.riverb.f.	88	42								o	o o			

FAMILY / Species	parts eaten	seed dispersal	seed predation	habit of plant	forest type	no. of food plants	no./km^2	J	F	M	A	M	J	J	A	S	O	N	D
Trichilia martiana C.DC.	aril	x		tree — 25m	h.mount.sav.f.+ h.riverb.f.	1*	0,5*				o o								
Trichilia quadrijuga H.B.K.	aril	x		tree — 25m	high forest	102	49		o o	o o									
Trichilia surinamensis (Miq.) C.DC.	whole fruit	x		tree — 30m	high forest, esp.on swampy places			o o											o o
MENISPERMACEAE																			
Abuta grandifolia (Mart.) Sandw.	mesocarp	x		liana	high forest, esp.at edges	4*	2*			o o							o	o	
MORACEAE																			
Bagassa guianensis Aubl.	unripe + ripe infruct.	x		tree — 45m	high forest	36	17	o o	o				o o	o	o y	o o y y	o o y y	o o y	o o
Brosimum lactescens (Sp.Moore) C.C. Berg	infruct.	x		tree — 35m	high forest + h.mount.sav.f.	32	15	o o										o o	o o
Brosimum parinarioides Ducke	infruct.	x		tree — 40m	high forest	12	6											o o	o
Cecropia sciadophylla Mart.	infruct. young leaves	x		tree — 30m	high forest (old treefall clearings)	40	19	o o	o o 1 1	o o	o o					o o	o o	o o	o o
Cecropia surinamensis Miq.	infruct.	x		tree — 25m	sec.f., at edges of high forest + h.mount.sav.f.	39	19	o o	o				o o					o o	o o
Clarisia racemosa R.et P.	whole fruit	x		tree — 40m	high forest	19	9					o o						o o	o
Coussapoa angustifolia Aubl.	infruct.	x		epiphytic tree/liana	high forest	15	7								o	o o	o o	o	
Coussapoa asperifolia Tréc.	infruct. pistillate inflorescences	x		epiphytic tree/liana	high forest	5	2							f f			o	o o	
Coussapoa latifolia Aubl.	infruct.	x		epiphytic tree /liana	high forest	87	41											o o	o o
Ficus americana ssp.guianensis	figs	x		epiphytic tree/liana	high forest, on swampy places	1*	0,5*												o
Ficus broadwayi Urb.	figs	x		epiphytic tree/liana	high forest	1*	0,5*											o	
Ficus citrifolia P. Miller	figs	x		treelet/ liana	l.mount.sav.f. on granite	1*	0,5*												o
Ficus gardneriana (vs. obtusifolia)	figs	x		liana	high forest (old treefall clearings)	1*	0,5*											o	
Ficus gomelleira Kunth et Bouche	figs	x		strangler	high forest	2*	1*					o	o						
Ficus insipida	figs	x		tree — 30m	high forest + pinaswamp	1*	0,5*									o	o		
Ficus malacocarpa	figs	x		epiph.tree/ strangler	high forest	1*	0,5*											o	

F A M I L Y / Species	parts eaten	seed dispersal	seed predation	habit of plant	forest type	no. of food plants	no./km^2	fruiting/flowering period(s)/time(s) of availability											
								J	F	M	A	M	J	J	A	S	O	N	D
Ficus nymphaeifolia P. Miller	figs	x		tree — 35m	high forest	2*	1*	o									o		
Ficus pertusa L.f.	figs	x		epiphytic tree — 35m	high forest + pinaswamp	1*	0,5*				o								
Ficus trigona L.f.	figs	x		epiph.tree/ strangler	high forest	1*	0,5*											o	
Ficus trigonata L.	figs	x		tree — 35m	high forest + h.mount.sav.f.	2*	1*				o o						o		
Helicostylis pedunculata R. Ben.	infruct.	x		tree — 25m	high forest	1	0,5									o	o		
Helicostylis tomentosa (P. et E.) Rusby	infruct.	x		tree — 30m	high forest	31	15				o o	o							
Maquira guianensis Aubl.	young leaves	-	-	tree — 20m	high forest	12	6					1				1			1
Perebea mollis (P. et E.) Hub.	infruct.	x		tree — 30m	high forest	1*	0,5*			o									
Pourouma minor R. Ben.	whole fruit	x		tree — 25m	high forest	64	31		o o										
Pourouma mollis Tréc.	whole fruit	x		tree — 25m	high forest + pinaswamp	33	16	o	o o										
Pourouma sp.	whole fruit	x		tree — 25m	high forest	-	-		o										
Trymatococcus oligandrus (Benoist) Lanj.	whole fruit	x		tree — 20m	high forest	1*	0,5*											o	
Trymatococcus paraensis Ducke	whole fruit	x		tree — 30m	high forest	1*	0,5*						o						
MYRISTICACEAE																			
Virola melinonii (R.Ben.) A.C. Smith	aril young leaves	x		tree — 30m	high forest	313	66	o o	o o	o o				1			o	o o	o o
Virola surinamensis (Rol.) Warb.	aril	x		tree — 35m	pinaswamp	32	15				o	o							
MYRTACEAE																			
Campomanesia aromatica (Aubl.) Griseb.	whole fruit	x		tree — 13m	h.mount.sav.f. esp.at edges (granite)	-	-	o	o										
Eugenia sp.	whole fruit	x		tree — 15m	h.riverb.f.	0	0	(o)											(o)
OLACACEAE																			
Minquartia guianensis Aubl.	whole fruit	x		tree — 25m	high forest	30	14							o	o				
ORCHIDACEAE																			
Two species	pseudobulbs	-	-	epiphytes	high forest	-	-						m						m
PALMAE																			
Attalea regia (Mart.) W. Boer	decaying leaf-bases	-	-	tree — 18m	edges of liana-forest, in poorly drained places	-	-	m m	m m	m m								m	m m

FAMILY / Species	parts eaten	seed dispersal	seed predation	habit of plant	forest type	no. of food plants	no./km^2	J	F	M	A	M	J	J	A	S	O	N	D
Euterpe oleracea Mart.	whole fruit	x		tree — 20m	pinaswamp, along creeks	loc.abundant						o	o o o						
Euterpe precatoria Mart.	whole fruit	x		tree — 27m	high forest	-	-									o	o o	o	
Oenocarpus bacaba Mart.	whole fruit	x		tree — 22m	high forest + at edges of it	67	32					o o	o o						
PASSIFLORACEAE																			
Passiflora glandulosa Cav.	whole fruit	x		liana	high forest, esp.at edges	-	-							o					
PIPERACEAE																			
Peperomia glabella (Sw.) A. Dietr.	young leaves	-	-	epiphyte	high forest, esp. on boughs of emergent trees	abundant		1 1						1	1 1	1 1	1 1	1 1	1 1
POLYGALACEAE																			
Moutabea guianensis Aubl.	mesocarp	x		liana	high forest	5	2	o o		o	o o	o		o o					
RUBIACEAE																			
Coussarea paniculata (Vahl) Standl.	whole fruit	x		tree — 12m	high forest	common					o	o							
Guettarda acreana Krause	whole fruit	x		tree — 15m	h.mount.sav.f. on granite	106	50					o o	o o						
Hillia illustris (Vell.) Schum.	flowers	-	-	epiphytic scrub in tree crowns	high forest	-	-												f
RUTACEAE																			
Fagara sp.	young leaves	-	-	tree — 15m	high forest	1*	0,5*										1	1 1	
SAPINDACEAE																			
Cupania sp.	whole fruit young leaves	x		liana	high forest	-	-										o o 1 1		
Paullinia acuminata Uitt.	aril	x		liana	high forest	-	-		o o										
Paullinia sphaerocarpa L.C. Rich. ex. Juss.	young seeds aril	 x	x	liana	high forest, h.riverb.f.	-	-	y y	y o	o o									y y
Paullinia spicata Benth.	aril	x		liana	high forest;esp. in pinaswamp	3*	1*		o				o						
Paullinia tricornis Radlk.	aril	x		liana	high forest	2*	1*							o	o o				
Talisia sylvatica (Aubl.) Radlk.	mesocarp	x		tree — 15m	high forest	-	-											o	

F A M I L Y / Species	parts eaten	seed dispersal	seed predation	habit of plant	forest type	no. of food plants	no./km²	J	F	M	A	M	J	J	A	S	O	N	D
SAPOTACEAE																			
Achrouteria pomifera Eyma	mesocarp	x		tree — 30m	h.mount.sav.f., high forest	19	9										o o	o o	
Chrysophyllum auratum Miq.	mesocarp	x		tree — 25m	h.mount.sav.f.	1*	0,5*		o										
Ecclinusa guianensis Eyma	mesocarp	x		tree — 25m	h.mount.sav.f. on granite + h.riverb.f.	363	173	o									o	o	o
Ecclinusa sp.	young seeds		x	tree — 30m	high forest	138	66		y y										
	mesocarp	x								o o	o o	o							
Micropholis guyanensis (A.DC.) Pierre	mesocarp	x		tree — 40m	high forest	0	0									(o o)			
Pouteria guianensis Aubl.	mesocarp	x		tree — 30m	high forest	9	4			o	o o								
Pouteria sp.	young seeds		x	tree — 30m	high forest	15	7												y y
	mesocarp	x						o o		o o									
SIMAROUBACEAE																			
Quassia simarouba L.f.	mesocarp bark	x		tree — 30m	high forest	53	25		o o								 b		
STERCULIACEAE																			
Guazuma ulmifolia Lam.	whole fruit/ mesocarp	x		tree — 25m	high forest	-	-									o			
Sterculia excelsa Mart.	flowers	-	-	tree — 33m	high forest	155	74								f				
STYRACACEAE																			
Styrax cf. fanshawei Sandw.	whole fruit/ mesocarp	x		tree — 40m	high forest	4*	2*			o	o o	o							
THUNBERGIACEAE																			
Mendoncia hoffmannseggiana Nees	mesocarp	x		liana	high forest, esp.at edges of clearings	-	-				o	o o	o o						
TILIACEAE																			
Apeiba echinata	flowers			tree — 35m	high forest	145	70										f	f f	
Gaertn.	mesocarp	x												o	o o	o o			
Apeiba glabra Aubl.	mesocarp	x		tree — 30m	high forest	54	26							o	o o	o o	o o		
Apeiba schomburgkii Szyszyl	mesocarp	x		tree — 20m	h.mount.sav.f.	4	2							o	o				
Apeiba tibourbou Aubl.	mesocarp	x		tree — 25m	h.mount.sav.f.	8	4									o o			

FAMILY / Species	parts eaten	seed dispersal	seed predation	habit of plant	forest type	no. of food plants	no./km²	J	F	M	A	M	J	J	A	S	O	N	D
ULMACEAE																			
Ampelocera edentula Kuhlmann	young leaves flowers mesocarp	x		tree — 20m	high forest	19	9		o								1	1 1 f	
VERBENACEAE																			
Vitex stahelii Moldenke	whole fruit/ mesocarp	x		tree — 45m	high forest, h.mount.sav.f., esp. edges of liana forest	72	34		o	o		o o	o o					o o	o
VIOLACEAE																			
Leonia glycycarpa R. et P.	mesocarp	x		tree — 20m	high forest, esp.in swampy places	1±	0,5±					o o							
VOCHYSIACEAE																			
Qualea dinizii Ducke	flowers	-	-	tree — 40m	high forest	50	24										f	f f	
FAMILY UNIDENTIFIED	whole fruit	x		tree or liana?	pinaswamp	2±	1±			o		o							
HONEY												m m		m					
INSECTA																			
Lepidoptera	caterpillars			in high trees	high forest					m m							m		
Isoptera	termites			on trunks of emergent trees	high forest			m		m	m m								
Larvae of pollinating and parasitic wasps in figs of different species				in figs				m			m m	m	m			m	m m	m m	m

Bignoniaceae (12 species), *Guttiferae* (9 species) and *Caesalpiniaceae* (8 species).
Ranked according to percentage of total feeding records, most important families were *Moraceae* (11.8%), *Mimosaceae* (11.6%), *Myristicaceae* (10.9%), *Sapotaceae* (8.6%), *Meliaceae* (5.8%) and *Burseraceae* (5.6%) (Table 3).

Table 2. Percentage of total food plant species used by *Ateles p. paniscus* for each food plant category

Habit	% Total food plant species (n = 207)
Tree	68.1
Liane/strangler	25.6
Twiner	1.0
Epiphyte	5.3

Table 3. The 58 plant families used by *Ateles p. paniscus* during the present study are ranked according to number of species eaten, and for each family the percentage of total feeding records is given. For this purpose, the three subfamilies of the *Leguminosae* are counted here as families, and the family Guttiferae is taken sensu lato

Family	No. of food spp.	% Total feeding records (n=2279)	Family	No. of food spp.	% Total feeding records (n=2279)
Moraceae	29	11.8	Orchidaceae	2	0.1
Mimosaceae (Legum.)	18	11.6	Sterculiaceae	2	0.2
Bignoniaceae	12	2.3	Capparaceae	1	1.0
Guttiferae	9	2.1	Caricaceae	1	0.1
Caesalpiniaceae (Legum.)	8	3.9	Combretaceae	1	0.05
Lecythidaceae	7	1.8	Dioscoreaceae	1	0.05
Meliaceae	7	5.8	Flacourtiaceae	1	2.2
Papilionaceae (Legum.)	7	2.4	Gesneriaceae	1	0.05
Sapotaceae	7	8.6	Gnetaceae	1	0.2
Celastraceae	6	1.1	Goupiaceae	1	0.05
Chrysobalanaceae	6	1.7	Humiriaceae	1	0.9
Sapindaceae	6	0.9	Loganiaceae	1	0.5
Annonaceae	5	3.6	Loranthaceae	1	0.05
Araceae	4	3.1	Marcgraviaceae	1	0.7
Burseraceae	4	5.6	Melastomataceae	1	0.6
Convolvulaceae	4	1.1	Menispermaceae	1	0.6
Palmae	4	0.9	Olacaceae	1	0.3
Tiliaceae	4	1.1	Passifloraceae	1	0.05
Boraginaceae	3	1.7	Piperaceae	1	0.4
Cactaceae	3	1.0	Polygalaceae	1	0.5
Euphorbiaceae	3	0.9	Rutaceae	1	0.1
Lauraceae	3	0.4	Simaroubaceae	1	0.2
Rubiaceae	3	0.5	Styracaceae	1	0.3
Anacardiaceae	2	0.8	Thunbergiaceae	1	0.1
Apocynaceae	2	0.7	Ulmaceae	1	0.7
Bombacaceae	2	1.8	Verbenaceae	1	0.6
Cucurbitaceae	2	1.2	Violaceae	1	0.05
Icacinaceae	2	0.3	Vochysiaceae	1	0.05
Myristicaceae	2	10.9	Unidentified	1	0.1
Myrtaceae	2	0.1			

Table 4. Food species used by *Ateles p. paniscus* , ranked according to the number of feeding records A - in the study period March 1976 - May 1978, and B - in the period of intensive autecological study (May 1977 - May 1978); C - gives the percentages of total number of feeding records over the entire study period (n = 2287)

Rank	Species	A	B	C
1	Virola melinonii	243	233	10.7
2	Guarea grandifolia	91	72	4.0
3	Ecclinusa guianensis	76	76	3.3
4	Cecropia sciadophylla	72	71	3.2
5	Dimorphandra multiflora	70	64	3.1
6	Bagassa guianensis	63	59	2.8
7	Inga edulis	60	60	2.6
8	Achrouteria pomifera	59	59	2.6
9	Inga alba	57	37	2.5
10	Tetragastris panamensis	56	48	2.5
11	Laetia procera	50	50	2.2
12	Ecclinus sp.	50	49	2.2
13	Philodendron scandens	39	34	1.7
14	Vataireopsis speciosa	36	36	1.6
15	Ephedranthus guianensis	34	33	1.4
16	Guatteria chrysopetala	32	32	1.4
17	Cordia lomatoloba	29	29	1.2
18	Tetragastris altis-	29	24	1.2
19	Inga bourgoni	27	27	1.1
20	Philodendron acutatum	26	25	1.1
21	Protium polybotryum	26	19	1.1
22	Clarisia racemosa	24	24	1.0
23	Couratari stellata	23	21	1.0
24	Ceiba pentandra	22	22	1.0
25	Rheedia macrophylla	22	20	1.0
26	Inga leiocalycina	22	13	1.0
27	Capparis maroniensis	22	6	1.0
28	Cayaponia ophthalmica	21	20	0.9
29	Sacoglottis cydonioides	21	13	0.9
30	Carapa procera	20	19	0.9
31	Ampelocera edentula	19	19	0.8
32	Bombax spectabile	19	18	0.8
33	Apeiba echinata	18	13	0.8
34	Clusia scrobiculata	17	15	0.7
35	Spondias mombin	17	14	0.7
36	Norantea guianensis	17	13	0.7
37	Geissospermum sp.	16	16	0.7
38	Licania micrantha	16	15	0.7
39	Brosimum parinarioides	16	13	0.7
40	Brosimum lactescens	16	12	0.7
41	Protium neglectum	16	8	0.7
42	Dicranostyles guianensis	15	9	0.6
43	Hylocereus sp. a.	14	14	0.6
44	Vitex stahelii	14	14	0.6
45	Abuta grandifolia	14	13	0.6
46	Bellucia grossularioides	14	13	0.6
47	Inga cf. capitata	14	12	0.6
48	Inga acreana	14	11	0.6
49	Adenocalymna sp.	13	13	0.6
50	Licania majuscula	13	13	0.6
51	Maytenus sp.	13	13	0.6
52	Coussapoa latifolia	13	9	0.6
53	Inga acrocephala	12	12	0.5
54	Moutabea guianensis	12	11	0.5
55	Strychnos tomentosa	11	11	0.5
56	Pourouma mollis	11	2	0.5
57	Arrabidaea courallina	10	10	0.4
58	Hyeronima laxiflora	10	10	0.4
59	Eperua falcata	10	9	0.4
60	Trichilia quadrijuga + T. surinamensis	10	9	0.4
61	Maripa scandens	9	9	0.4
62	Pterocarpus officinalis + P. vs. santalinoides	9	7	0.4
63	Helicostylis tomentosa	9	4	0.4
64	Dystictis vs. granulosa	8	8	0.3
65	Ficus gardneriana	8	8	0.3
66	Guettarda acreana	8	8	0.3
67	Peperomia glabella	8	8	0.3
68	Attalea regia	7	7	0.3
69	Cordia sagotii	7	7	0.3
70	Guarea kunthiana	7	7	0.3
71	Unonopsis glaucopetala	7	7	0.3
72	Euterpe oleracea	7	6	0.3
73	Cayaponia rigida	7	5	0.3
74	Duguetia sp.	7	5	0.3
75	Minquartia guianensis	7	2	0.3
76	Newtonia suaveolens	6	6	0.3
77	Parinari excelsa	6	6	0.3
78	Pereskia aculeata	6	6	0.3
79	Styrax cf. fanshawei	6	6	0.3
80	Eschweilera poiteaui	6	5	0.3
81	Leretia cordata	6	5	0.3
82	Xylophragma seemannianum	5	5	0.2

Table 4 (continued)

Rank	Species	A	B	C
83	Cheiloclinium sp.249	5	5	0.2
84	Drypetes variabilis	5	5	0.2
85	Helicostylis pedunculata	5	5	0.2
86	Ocotea wachenheimii	5	5	0.2
87	Parkia nitida	5	5	0.2
88	Parkia pendula	5	5	0.2
89	Paullinia acuminata	5	5	0.2
90	Pouteria sp. 400	5	5	0.2
91	Virola surinamensis	5	5	0.2
92	Paullinia spicata	5	4	0.2
93	Tabebuia serratifolia	5	4	0.2
94	Honey	5	2	0.2
95	Quassia simarouba	5	1	0.2
96	Apeiba glabra	4	4	0.2
97	Gustavia hexapetala	4	4	0.2
98	Hylocereus sp. b.	4	4	0.2
99	Inga pezizifera	4	4	0.2
100	Inga rubiginosa	4	4	0.2
101	Oenocarpus bacaba	4	4	0.2
102	Gnetum urens	4	3	0.2
103	Paullinia sphaerocarpa	4	3	0.2
104	Dialium guianense	4	2	0.2
105	Eschweilera corrugata	4	2	0.2
106	Couepia caryophylloides	4	0	0.2
107	Alchorneopsis floribunda	3	3	0.1
108	Caterpillars (2 spp.)	3	3	0.1
109	Cedrela odorata	3	3	0.1
110	Cheiloclinium podostemum	3	3	0.1
111	Clusia grandiflora	3	3	0.1
112	Maquira guianensis	3	3	0.1
113	Perebea mollis	3	3	0.1
114	Philodendron sp.	3	3	0.1
115	Pouteria guianensis	3	3	0.1
116	Termites	3	3	0.1
117	Dipteryx odorata	3	2	0.1
118	Stizophyllum inaequilaterum	3	2	0.1
119	Hymenolobium petraeum	3	2	0.1
120	Mendoncia hoffmannseggiana	3	2	0.1
121	Pithecellobium jupunba	3	2	0.1
122	Paullinia tricornis	3	1	0.1
123	Pourouma minor	3	0	0.1
124	Coussapoa angustifolia	2	2	0.1
125	Coussapoa asperifolia	2	2	0.1
126	Coussarea paniculata	2	2	0.1
127	Fagara sp.	2	2	0.1
128	Ficus broadwayi	2	2	0.1
129	Ficus gomelleira	2	2	0.1
130	Ficus trigonata	2	2	0.1
131	Guazuma ulmifolia	2	2	0.1
132	Jacaratia spinosa	2	2	0.1
133	Licaria canella	2	2	0.1
134	Malmea obovata	2	2	0.1
135	Monstera adansonii	2	2	0.1
136	Platymiscium ulei	2	2	0.1
137	Sterculia excelsa	2	2	0.1
138	Talisia sylvatica	2	2	0.1
139	Trichilia martiana	2	2	0.1
140	Unidentified species	2	2	0.1
141	Cheiloclinium cognatum	2	1	0.1
142	Orchidaceae (2 spp.)	2	1	0.1
143	Pourouma sp.	2	0	0.1
144	Bignoniaceae sp. b.	1	1	0.05
145	Bignoniaceae sp. c.	1	1	0.05
146	Campomanesia aromatica	1	1	0.05
147	Cecropia surinamensis	1	1	0.05
148	Cedrelinga cateniformis	1	1	0.05
149	Cheiloclinium sp. 3549	1	1	0.05
150	Clusia sp.	1	1	0.05
151	Combretum rotundifolium	1	1	0.05
152	Cordia panicularis	1	1	0.05
153	Couratari guianensis	1	1	0.05
154	Cupania sp.	1	1	0.05
155	Cynometra marginata	1	1	0.05
156	Dioclea macrocarpa	1	1	0.05
157	Dioscorea trifida?	1	1	0.05
158	Enterolobium schomburgkii	1	1	0.05
159	Eschweilera congestiflora	1	1	0.05
160	Euterpe precatoria	1	1	0.05
161	Ficus americana	1	1	0.05
162	Ficus citrifolia	1	1	0.05
163	Ficus malacocarpa	1	1	0.05
164	Ficus nymphaeifolia	1	1	0.05
165	Ficus pertusa	1	1	0.05
166	Ficus trigona	1	1	0.05
167	Gesneriaceae (1 sp.)	1	1	0.05
168	Hillia illustris	1	1	0.05
169	Inga stipularis	1	1	0.05
170	Leonia glycycarpa	1	1	0.05
171	Leretia sp.	1	1	0.05
172	Licania densiflora	1	1	0.05
173	Loranthaceae (1 sp.)	1	1	0.05
174	Maripa glabra	1	1	0.05
175	Tanaecium jaroba	1	1	0.05
176	Nectandra cf. kunthiana	1	1	0.05

Table 4 (continued)

Rank	Species	A	B	C	Rank	Species	A	B	C
177	Operculina alata	1	1	0.05	191	Clusia platystigma	1	0	0.05
178	Parahancornia amapa	1	1	0.05	192	Clusia purpurea	1	0	0.05
179	Parinari campestris	1	1	0.05	193	Copaifera epunctata	1	0	0.05
180	Platonia insignis	1	1	0.05	194	Copaifera guianensis	1	0	0.05
181	Qualea dinizii	1	1	0.05	195	Eperua rubiginosa	1	0	0.05
182	Symphonia globulifera	1	1	0.05	196	Eugenia sp.	1	0	0.05
183	Trymatococcus oligandrus	1	1	0.05	197	Ficus insipida	1	0	0.05
					198	Goupia glabra	1	0	0.05
184	Trymatococcus paraensis	1	1	0.05	199	Inga coriacea	1	0	0.05
					200	Inga thibaudiana	1	0	0.05
185	Anacardium giganteum	1	0	0.05	201	Lecythis davisii	1	0	0.05
186	Apeiba schomburgkii	1	0	0.05	202	Micropholis guyanensis	1	0	0.05
187	Apeiba tibourbou								
188	Bignoniaceae sp. a.	1	0	0.05	203	Ormosia paraensis	1	0	0.05
189	Cheiloclinium cf. gleasonianum	1	0	0.05	204	Passiflora glandulosa	1	0	0.05
190	Chrysophyllum auratum	1	0	0.05	205	Peltogyne venosa	1	0	0.05
					206	Rheedia benthamiana	1	0	0.05
					207	Tabebuia capitata	1	0	0.05

Table 5. Most important genera providing food species for Ateles p. paniscus, ranked according to the percentages of total number of feeding records

Genus	No. of species	% Total feeding records (n=2287)
Virola (Myristicaceae)	2	10.9
Inga (Mimosaceae)	12	9.5
Ecclinusa (Sapotaceae)	2	5.5
Guarea (Meliaceae)	2	4.3
Tetragastris (Burseraceae)	2	3.7
Cecropia (Moraceae)	2	3.2
Dimorphandra (Caesalpiniaceae)	1	3.1
Philodendron (Araceae)	3	3.0
Bagassa (Moraceae)	1	2.8
Achrouteria (Sapotaceae)	1	2.6
Laetia (Flacourtiaceae)	1	2.2

Of all food species recorded, Virola melinonii (Myristicaceae) seems to be the most important one with 10.7% of total number of feeding records, followed by Guarea grandifolia (Meliaceae) with 4.0%, Ecclinusa guianensis (Sapotaceae) with 3.3%, Cecropia sciadophylla (Moraceae) with 3.2%, Dimorphandra multiflora (Caesalpiniaceae) with 3.1%, Bagassa guianensis (Moraceae) with 2.8%, Inga edulis (Mimosaceae) and Achrouteria pomifera (Sapotaceae) with 2.6%, Inga alba (Mimosaceae) and Tetragastris panamensis (Burseraceae) with 2.5%.

About 85 species were recorded only once or twice during the study period, so less than 0.1% of total feeding records (Table 4).

Among the genera, *Virola* also comes first with 10.9% of total feeding records, followed by *Inga* (9.5%), *Ecclinusa* (5.5%), *Guarea* (4.3%), *Tetragastris* (3.7%), *Cecropia* (3.2%), *Dimorphandra* (3.1%), *Philodendron* (3.0%), *Bagassa* (2.8%), *Achrouteria* (2.6%) and *Laetia* (2.2%) (Table 5).

Ateles p. paniscus is predominantly frugivorous, feeding on fruits in 82.9% of total feeding records (n = 2287) (Fig. 8).
Flowers and leaves play a minor role in the overall diet of spider monkeys, counting for 6.4% and 7.9% respectively, but seasonally can be important. Other foods eaten by spider monkeys were bark (1.7%), decaying wood (0.3%), pseudobulbs (0.1%), aerial roots (0.2%), honey (0.2%), termites (0.1%) and caterpillars (0.1%).

4.1.1. *Fruits*. In total, *A. p. paniscus* was feeding on 171 kinds of fruit. Besides berries, drupes, pods and capsules, also infructescences with the fruits adnate to the enlarged receptacle or to the fleshy perianth (like in several *Moraceae*) forming the major edible part, figs and compound fruits are referred to as fruits. Fruits can be dehiscent or indehiscent, dry or pulpy, the outer layer can be thin, leathery or woody.

Fruits consumed by spider monkeys ranged from the tiny globose drupes of *Hyeronima laxiflora* (Euphorbiaceae), 0.3 - 0.5 cm in diameter, to the woody, thick-walled, operculate fruits of *Lecythis davisii* (Lecythidaceae) that grow to about 20 cm in diameter, or to the leathery elongate pods of *Cedrelinga cateniformis* (Mimosaceae) that range from 40 to 80 cm in length.

As a rule, spider monkeys didn't spoil energy and time in selectively feeding on particular parts of fruits, but swallowed whole fruits or, in the case of a thick or tough outer layer (exocarp or pericarp), they tended to bite it open and to swallow the contents (pulp including seeds, or seed(s)/stone(s) surrounded by an edible layer of mesocarp or an edible aril). In many fruit species the layer of mesocarp or the aril is strongly attached to the seed/stone (e.g., in all *Burseraceae* and *Inga*), and hard to separate. This may be an adaptation of the plant species to dispersal by specialized frugivorous birds and mammals like *Ateles*. Most other Surinam monkey species, when feeding on fruits of this kind, spit out the seed(s) or stone(s) after chewing or sucking off the edible part. In many cases they damage the seeds, wasting them for germination.
Spider monkeys swallowed whole fruits in 25.2% of total fruit feeding records (39.3% of total fruit species eaten). They dropped the outer layer and swallowed the mesocarp or aril (mostly including seeds or stones) in 68.2% of total fruit feeding records (44.7% of total fruit species eaten) (Table 6). Young seeds or part of it (e.g., the plumula in *Eperua*) were consumed in 3.7% of total fruit feeding records (13.7% of total fruit species eaten). Fruits of some genera, like *Licania*, *Couepia* and *Gnetum*, were eaten by scraping off the exo- and mesocarp/pericarp/perigonium, and dropping the seed/stone (1.5% of total fruit feeding records; 4.2% of total fruit species eaten).
Furthermore, spider monkeys fed exclusively on the exocarp in young fruits of *Ceiba pentandra* (0.3%; 0.6%), on the young columella of *Cedrela odorata* (0.2%;0.6%), the pseudofruit (= fleshy pedicel) of *Anacardium giganteum* (0.1%; 0.6%) and the juice of *Geissospermum* sp. (0.9%; 0.6%), dropping the rest of the fruit.

Fruits and seeds: seed predation vs. seed dispersal and seed dropping.
It is important to distinguish between ingestion of seeds and digestion of seeds. Spider monkeys mostly swallow seeds intact without mastication and the seeds pass through the digestive tract without losing their power of germination. In addition, seeds are sometimes dropped after the softer, edible parts have been removed from them with the hands or mouth.
On the other hand, seeds of certain families, like the *Lecythidaceae*, are eaten in an unripe stage. After extracting these young seeds from the fruit, they are chewed into a mealy pulp and digested. Such behaviour is

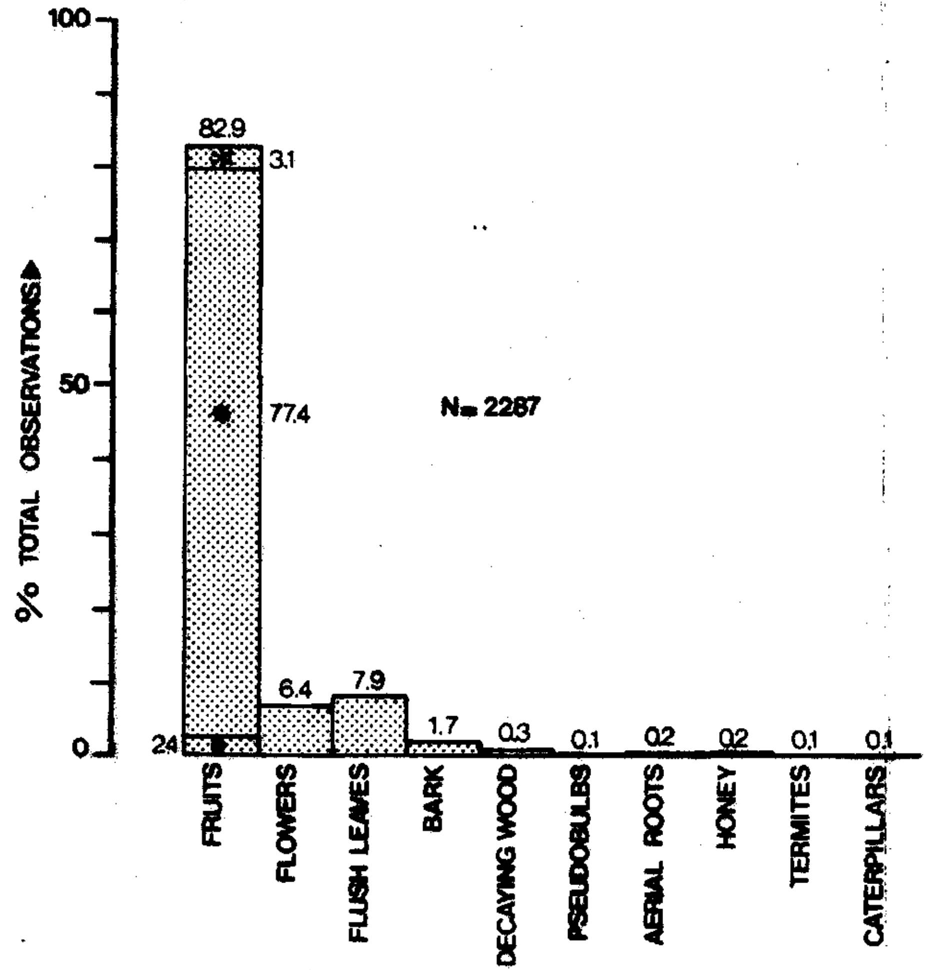


Fig. 8. Annual utilization of different foods in Ateles p. paniscus, expressed as the percentage of the total number of feeding records for each food category. ✱ = seeds predated, ✸ = seeds dispersed endozoochorically, ● = seeds dropped.

Table 6. A - Percentage of total number of fruit species eaten for any part of fruit, B - percentage of total number of food species eaten for any part of food plants, C - percentage of total number of fruit feeding records for any part of fruit, and D - percentage of total number of feeding records for any part of food plants and miscellaneous, used by *Ateles p. paniscus*

Parts eaten	No. of species used	A %Total fruit species (n=171)	B %Total food species (n=207)	C %Total fruit feeding records (n=1895)	D %Total feeding records (n=2287)
Whole fruit/infruct./ fig swallowed	66	39.3	31.9	25.2	20.9
Mesocarp (exocarp dropped, seed(s) ingested)	50	29.8	24.1	43.8	36.3
Aril (exocarp dropped, seeds ingested)	25	14.9	12.0	24.4	20.2
Young seeds/plumula ± young aril	23	13.7	11.1	3.7	3.1
Exo+mesocarp/pericarp/ perigonium (seeds dropped)	7	4.2	3.3	1.5	1.3
Exocarp (rest of fruit dropped)	1	0.6	0.5	0.3	0.2
Juice (chewed fruit dropped)	1	0.6	0.5	0.9	0.7
Columella (± young seeds)	1	0.6	0.5	0.2	0.1
Pseudofruit (fleshy pedicel)(fruit dropped)	1	0.6	0.5	0.1	0.05
Flowers/inflorescences/ floral buds	33		16.0		6.4
Young leaves/shoots/ petioles	28		13.5		7.9
Pseudobulbs (fleshy thickened stems of certain orchids)	2		1.0		0.1
Aerial roots	2		1.0		0.2
Bark	11		5.3		1.7
Decaying wood (rotten sheaths of *Attalea regia*)	1		0.5		0.3
Honey	-		-		0.2
Caterpillars	2		-		0.1
Termites	1		-		0.1

referred to as seed predation because the seeds obviously are destructed. Swallowing seeds and excreting them intact (*endoozoochory*) results in seed dispersal. When seeds are removed from the fruit and dropped, this behaviour is referred to as seed dropping. When the monkeys drop seeds out of the fruiting tree, these seeds are not dispersed any more than would be the case when they fell by themselves out of the tree.

However, in some cases the monkeys may carry fruits away from the fruiting tree over considerable distances before eating them and dropping the seeds intact. For sure, this is a case of dispersal (*exozoochory*), but for the sake of convenience I include these rare cases under seed dropping.

Spider monkeys consumed fruits in a ripe stage in 96.0% of total fruit feeding records (150 species; n = 1902). Seed dispersal took place in 93.5% of total fruit feeding records (138 species), and seed dropping was recorded in 2.7% of total fruit feeding records (10 species). Parts of young fruits were eaten only in 4.0% of total fruit feeding records (24 species), whereas seed predation was recorded in 3.7% of total fruit feeding records (23 species) (Table 7).

Table 7. A - Percentage of total number of fruit species eaten, and B - percentage of total number of fruit feeding records, for seed dispersal fruit feeding, seed predation fruit feeding and seed dropping fruit feeding in *Ateles p. paniscus*

	No. of fruit species	%Total fruit species (n = 171)	%Total fruit feeding records (n = 1902)
Seed dispersal	138	80.7	93.5
Seed predation	23	13.5	3.7
Seed dropping	10	5.8	2.7

As shown in Fig. 8, seed predation was recorded in 3.1%, seed dispersal in 77.4% and seed dropping in 2.4% of total feeding records (n = 2287).

Ateles as seed disperser. Seeds dispersed by spider monkeys ranged from the tiny seedlets of many *Moraceae* (e.g., *Bagassa*, *Cecropia*, *Coussapoa*, *Ficus*) to the big ellipsoid seeds of *Platonia insignis* (Guttiferae), measuring up to 4 x 2 cm.

Generally, the faeces of spider monkeys, dropped out of a tree, fall apart by lack of a binding substance and thus seeds and stones are spread widely over the forest floor. Seeds and stones, dispersed in this way by spider monkeys, usually don't attract terrestrial seed predators. In contrast, the faeces of *Alouatta* are very compact, sometimes containing up to several hundreds of seeds/stones, kept together by undigested leaf mulch. It heaps up at one place, as such and by its smell attracting seed predators to the place.

Many fruiting trees, used by monkeys, attract terrestrial seed predators like agoutis, acouchis, deer and peccaries, when their fruits fall in quantity. Also other animals, like bruchid weevils (*Bruchidae*), several terrestrial birds and tortoises are attracted by the fruits dropped out of these trees. Especially, curassows (*Crax alector*) and trumpeters (*Psophia crepitans*) seem to be attracted by crashing sounds and vocalizations of *Ateles*, and frequently feed on the fruits accidently dropped by the monkeys. By analysing stomach contents of many curassows and trumpeters, it appeared that almost all seeds and stones ingested are more or less damaged by either the bill or by grinding. Consequently, these birds do not act as seed dispersers.

Analysis of many dung samples of tortoises that were found in the Voltzberg study area, learned that these animals can act as seed dispersers at least for several species (e.g., *Tetragastris* spp., *Protium* spp., *Spondias mombin*, *Gurania* spp. and *Ecclinusa guianensis*). However, in contrast with *Ateles*, these animals swallow only small amounts of fruits and their day ranges are small.

Ateles p. paniscus appears to be an important seed disperser for many species and in several species that are not eaten by specialized frugivorous birds (like cotngids, toucans and guans), *Alouatta* nor *Geochelone*, it seems to be the only disperser. Where seed predation by other monkeys, insects, birds and terrestrial animals is strong, the plant's dispersal may be completely dependent on *Ateles*. Most obviously this was the case in the following species: *Capparis maroniensis*, *Sacoglottis cydonioides*, *Gustavia hexapetala*, *Dimorphandra multiflora*, *Guarea kunthiana*, *Guarea grandiflora*, *Trichilia* spp., *Brosimum parinarioides*, *Clarisia racemosa*, *Minquartia guianensis*, *Ecclinusa guianensis*, *Ecclinusa* sp. The phenomenon is nicely demonstrated in fruiting *Brosimum parinarioides* (Moraceae), a widely dispersed tree (Appendix, no. 98), not common in the Voltzberg study area. First of all *Chiropotes satanas*, an important seed predator, visited a particular tree regularly over several months, feeding on the young seeds in many stages. Occasionally, also macaws and squirrels fed on the young seeds. When maturing, still many fruits were hanging in the tree. Except for *Ateles*, who swallowed the fruits as a whole, also other monkeys like *Saimiri sciureus*, *Cebus apella* and *Cebus nigrivittatus* were seen feeding on the pulp, dropping the mature seeds. Because of abundant fruiting, also many fruits fell down spontaneously, in particular when the monkeys were moving through the crown.

While *Ateles* or other monkeys were feeding on this tree, already several terrestrial seed predators were seen coming into the area to feed on the fallen seeds, e.g., several agoutis, deer (*Mazama americana*), and sometimes peccaries. Also curassows and trumpeters were seen feeding on the pulp of fallen fruits and swallowing the seeds. At that moment, still hundreds of seeds could be seen lying under the tree on the forest floor. Next day, all seeds were gone and no one could be found anymore. All mature seeds, dropped on the forest floor, were either predated or buried by scatter hoarding rodents (e.g., agoutis). In this particular case, the tree may depend completely on *Ateles* for its dispersal.

4.1.2. *Flowers*. Flowers are contributing only a small portion to the spider monkey diet. In total, *Ateles p. paniscus* was feeding on 33 species of flower (16% of total food plant species recorded) in 6.4% of total feeding records (Table 6; Fig. 8).

Of the 33 species producing edible flowers, 17 were trees, 13 lianes and 3 epiphytes. Ranked according to the percentage of total flower feeding records, the most important family was *Bignoniaceae* (25.9%; 11 species), followed by *Meliaceae* (17.7%; 2 species), *Marcgraviaceae* (11.6%; 1 species), *Cactaceae* (10.9%; 3 species), *Bombacaceae* (9.5%; 2 species), *Mimosaceae* (6.8%; 4 species), *Ulmaceae* (4.8%; 1 species), *Tiliaceae* (2.7%; 1 species), *Caesalpiniaceae* (2.0%; 1 species), *Guttiferae* (1.4%; 2 species), *Papilionaceae* (1.4%; 1 species), and *Moraceae*, *Rubiaceae*, *Sterculiaceae* and *Vochysiaceae* (0.7%; 1 species).

Most of the flowers were consumed mature or at a stage just before opening. When small, the whole flower or inflorescence would be swallowed (e.g., *Ampelocera edentula*, *Carapa procera*, *Enterolobium schomburgkii* and *Newtonia suaveolens*), but most flowers were eaten only partly. Especially, corolla and/or tips of petals were preferred in many species (esp. so in *Bignoniaceae*), while dropping the calyx or without picking off the rest of the flower from the peduncle, stem or twig. Several species were used only for the tips of stamens, style and/or for the stigma (*Bombax spectabile*, *Hylocereus* spp., *Pereskia aculeata* and *Parkia* spp.), some for the sticky central body of staminodes (*Clusia* spp.), for the bracts transformed in honeycups (*Norantea guianensis*) or for the thickened perianth (like in pistillate inflorescences of *Coussapoa*).

Ranked according to the percentage of total flower feeding records, most important species were *Guarea grandifolia* (13.6%), *Norantea guianensis* (11.6%), *Hylocereus* sp. a. and *Adenocalymna* sp. (8.8%), *Bombax spectabile* (7.5%), *Arrabidaea courallina* (6.8%), *Ampelocera edentula* (4.8%), *Newtonia suaveolens* (4.1%), *Carapa procera* (4.1%) and *Xylophragma seemannianum* (3.4%). The other 23 species contributed less than 3% in total flower feeding records.

4.1.3. *Leaves*. Like flowers, leaves are only contributing a small portion to the spider monkey's diet. In total, it was feeding on 28 species of leaf (13.5% of total food plant species recorded) in 7.9% of total feeding records (Table 6;Fig. 8).

Of the 28 plant species producing edible leaves, 19 were trees, 4 lianes, 1 twiner and 4 epiphytes. Ranked according to the percentages of total leaf feeding records, most important family was *Papilionaceae* (29.7%; 4 species), followed by *Araceae* (25%; 3 species), *Bombacaceae* (12.2%; 2 species), *Meliaceae* (5.8%; 1 species), *Bignoniaceae* and *Moraceae* (4.7%; 2 species), *Piperaceae* (4.7%; 1 species), *Caesalpiniaceae* (3.5%; 2 species), *Ulmaceae* (2.3%; 1 species), *Mimosaceae* (1.2%; 1 species), *Lauraceae* (1.2%; 1 species), and *Myristicaceae*, *Chrysobalanaceae*, *Rutaceae*, *Caricaceae*, *Sapindaceae*, *Dioscoreaceae*, *Gesneriaceae* and *Loranthaceae* (0.6%; 1 species).

It has to be emphasized that spider monkeys exclusively fed on young (flush) leaves during the present study. They never were seen consuming one mature leaf. In many cases only the apex of flush leaves was eaten (e.g., *Bombax spectabile*, *Ceiba pentandra*, *Jacaratia spinosa*, *Tabebuia serratifolia* and *Cecropia sciadophylla*), or parts of the lamina were ripped off of the costa with the mouth (e.g., *Ceiba pentandra*, *Bombax spectabile*).

Besides flush leaves, also young shoots and young leaves, still rolled up in the sheath, were eaten (like in *Philodendron scandens* and *P. acutatum*) and sometimes the base of the petiole (like in *Philodendron scandens* and *Carapa procera*).

Ranked according to the percentages of total leaf feeding records, most important species were *Vataireopsis speciosa* and *Philodendron scandens* (both 20.9%), followed by *Ceiba pentandra* (8.1%), *Carapa procera* (5.8%), *Pterocarpus officinalis* + *P.* vs. *santalinoides* (5.2%), *Peperomia glabella* (4.7%), *Bombax spectabile* (4.1%) and *Philodendron acutatum* (3.5%). The other 20 species contributed less than 3% in total leaf feeding records.

4.1.4. *Pseudobulbs*. Pseudobulbs are the thickened, fleshy stems of certain *Orchidaceae*, mostly epiphytes, that function as food and water reserve. Spider monkeys were seen feeding on parts of pseudobulbs, while dropping the leaves and mostly part of the plant, in two epiphytic species of orchids, growing on boughs high up in tall trees. They contributed only 1% in total food plant species recorded and only 0.1% in total feeding records (Table 6; Fig. 8). Both species were not identifiable by means of the collected sterile samples, but seemed to be quite abundant in the Voltzberg study area.

4.1.5. *Aerial roots*. Aerial roots are the roots growing out of the stems of certain plants and hanging down in the air. When reaching the ground, they sometimes take hold in the forest soil and start to act as normal roots. Many tropical epiphytes form aerial roots. Spider monkeys were seen feeding on the tips of aerial roots of two species of *Araceae* (*Philodendron acutatum* and *P. scandens*). To reach the tip of these pendent aerial roots, the monkeys had to pull up several meters of it. The two species contributed only 1% in total food plant species recorded and 0.2% in total feeding records (Table 6; Fig. 8).

4.1.6. *Bark and decaying wood*. In total, *Ateles p. paniscus* was feeding on the bark of 11 species (5.3% of total food plant species recorded), in 1.7% of all feeding records (Table 6; Fig. 8). All species were trees. Ranked according to the percentages of total bark-feeding records, the most important species was *Licania micrantha* (37.5%), followed by *Inga alba* (30.0%), *Sacoglottis cydonioides* (10.0%), *Inga leiocalycina* (5.0%) and the other 7 species (2.5% each).

Spider monkeys seemed to prefer decaying bark. Because almost all trees used were healthy, the edges of scars, waterholes and certain patches at the underside of boughs were selected in particular. These patches, not always easily to reach, have a softer, more or less decaying texture, caused by the rain water flowing down from boughs and trunk or out of holes, keeping these particular places wetter than other ones.

The last item eaten occasionally and apparently only by some adults, were the rotten sheaths of long before shed leaves of the palm *Attalea regia*, found under the crown just above the smooth trunk. Only adults were seen feeding occasionally on this item. Especially an old female was seen several times entering low forest at the edge of liane forest or 'rock savanna', where this palm frequently occurs, to feed on this rotten palm wood. The material, looking at a distance like peat, was consumed palatably and with handfuls. This food was taken in only 0.3% of all feeding records (Table 6; Fig. 8).

4.1.7. *Honey*. Occasionally, spider monkeys were seen feeding on honey from bees nests in tree holes. This occurred in only 0.2% of the total number of feeding records (Table 6; Fig. 8). The monkeys obtained honey by reaching with one hand into the hole and licking the honey off of the finger-tips. The holes were difficult to reach and the monkeys had often to climb down big trunks for that.

4.1.8. *Insects*. Spider monkeys were definitively seen feeding on insects in a few cases. At least two species of small caterpillars were seen eaten, in 0.1% of all feeding records. Both species have been collected, but were not identifiable. The caterpillars were found in clumps of several hundreds, attached by web to a leaf.

Spider monkeys were seen eating one species of termites in 0.1% of the total number of feeding records (Table 6; Fig. 8). Usually, they opened the tunnels of termites running up the huge bole of an emergent tree (esp. of the species *Hymenolobium flavum*) and waited till a number of termites walked into the open. With the tongue they seemed to pick out only certain types of termites. Whether they selected workers or soldiers was not clear. Spider monkeys were never seen opening termites nests that sometimes occur high up in the crowns.

Except for actively feeding on insects, spider monkeys accidently ingest minute insects, like all stages of pollinating and parasitic wasps present in all kinds of figs. In general, *Ficus* spp. were rare and widely dispersed in the Voltzberg study area. In total, 11 species of fig were eaten, contributing together only 1% in the total number of feeding records.

Probably, the animal protein intake of *Ateles p. paniscus* is restricted to the above mentioned cases. It never fed on rotten fruits, usually containing animal life. Wormy fruits were dropped too.

4.2. Seasonal Variation

4.2.1. *Phenology*. Phenological data on many trees and lianes, and particularly on food plants of *Ateles*, were collected continuously over a period of two years in the Voltzberg study area, and scored in two-week periods. The data on food plants are compiled in Table 1.

In general, flowering and fruiting periods seem to be seasonal. One important exception is *Ficus*, of which most of the species do not seem to show any tendency to seasonality. Some obvious parameters for seasona-

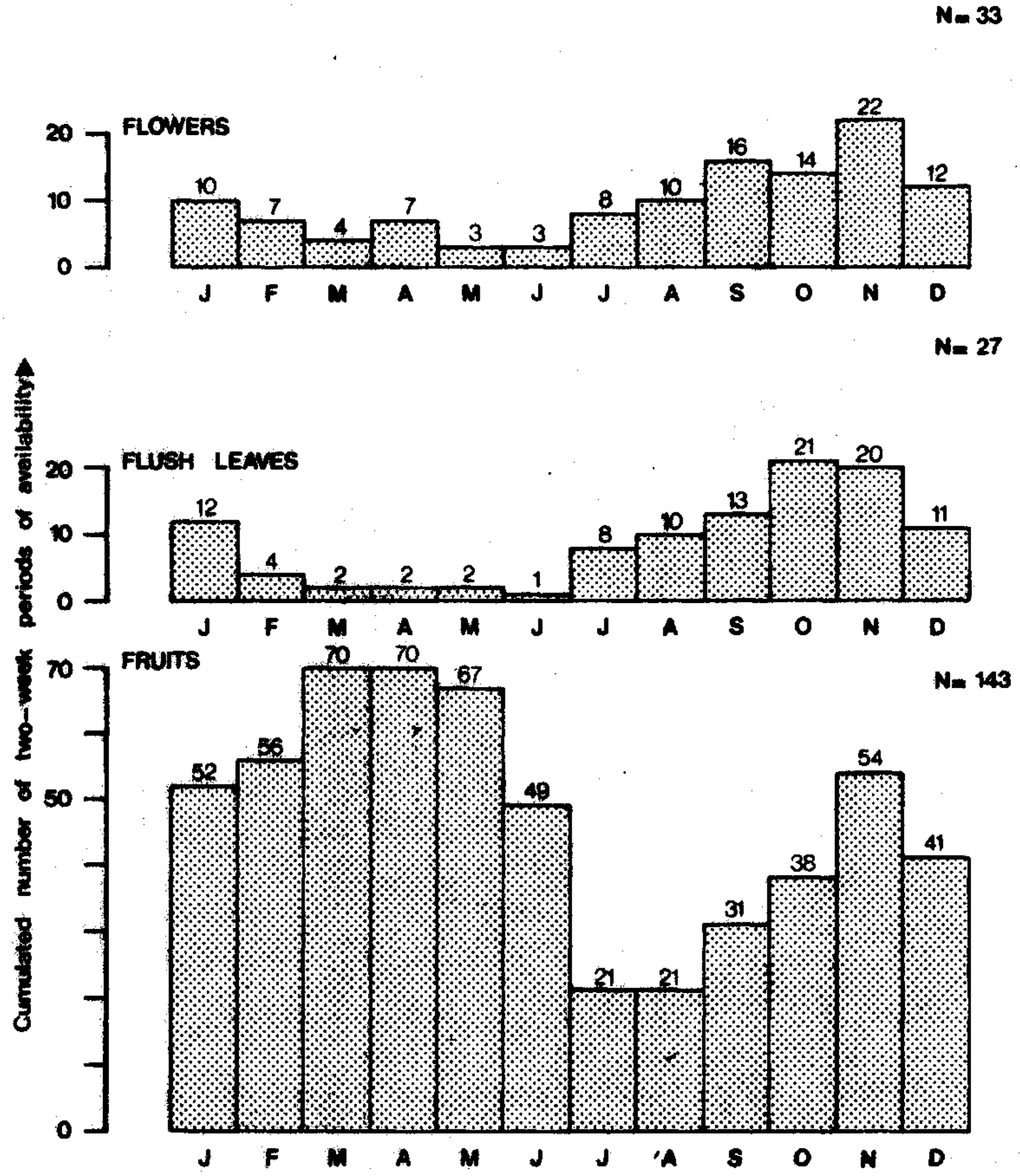


Fig. 9. Monthly variation in availability of edible flowers, flush leaves and ripe fruits for spider monkeys in the Voltzberg study area during the present study, expressed as the sum of two-week periods in which the items were available. Only those species for which phenological data were collected systematically throughout the year were taken into account, resulting in 33 species for flowers, 27 for leaves and 143 for fruits.

lity of flowering, flushing and fruiting can be extracted from Table 1. As shown in Fig. 9, at the beginning of the long dry season (July/August) many trees and lianes start to flower, some after dropping their leaves. The flowering season lasts from the end of July to February with a distinct peak in November, so towards the start of the short wet season. A minor peak can be seen in April, at the end of the short dry season. During the long wet season, very few plants are flowering.

Flushing of leaves gives a somewhat similar pattern of seasonality. Flushing in trees and lianes starts at the end of July and lasts till February, showing a peak in October/November, towards the end of the long dry season. From February to July, flushing seems to be rare.

Ripe fruits are available throughout the year, but a distinct peak can be seen in the months March, April and May. Towards the end of the long wet season the availability of ripe fruits drops drastically, with a minimum in July and August. A minor peak can be seen in November, at the start of the short wet season.

Most tree species tend to fruit every year. However, flowering and fruiting periods of a particular species can vary considerably from year to year, maybe because of yearly variations in timing and duration of the different seasons and/or differences in rainfall. A shift of one or two months is not unusual, sometimes even more (e.g., Bombax spectabile was flowering in 1977 from mid-June to mid-August, in 1978 from March to May). Moreover, individuals of some species seem to fruit only once in two years, or even once in three or four years (e.g., Hymenolobium spp.). Some years, the whole fruit crop of a species may fail for some reason (e.g., Minquartia guianensis in 1977, Capparis maroniensis in 1978).

Many lianes seem to fruit without any tendency to seasonality (e.g., Strychnos spp., Ficus spp., Moutabea guianensis), and some trees (e.g., Guarea grandifolia, Ficus spp.) and lianes (e.g., Ficus spp., Abuta grandifolia) do fruit about twice a year.

In some species fruits are present over prolonged periods (e.g., Capparis maroniensis 4 months, Dimorphandra multiflora 7 months, Licania majuscula 5 months, Virola melinonii 5 months), since the individual trees are not fruiting synchronously, whereas other species provide the monkeys with ripe fruits only during two weeks (e.g., Ampelocera edentula, several Ficus spp.).

4.2.2. Monthly variation in food choice. In Fig. 10, the monthly variation in food choice of Ateles p. paniscus is shown. The striking variation in record numbers per month is due to the fact that the activity pattern of spider monkeys could vary strongly. The spread in activities was positively correlated to the total number of food species available. In August, for instance, a total of only 45 feeding records was collected, caused by long resting periods and few feeding periods concentrated on a small number of food plants. A total of only 24 food species was used during August, whereas in the period September - June between 41 and 61 food species were used monthly.
It has to be emphasized that the total number of observation hours for each month of the year was kept almost the same (about 75 hours).

Fruits. Fruits account for a relatively small percentage (less than 60%) of total feeding records for each month during the first part of the long dry season (July, August and September). As shown in Fig. 9, this period is characterized by a striking decline in the availability of edible fruits. During the months January - July, fruits account for a high percentage of total feeding records, with a maximum in May/June (over 95%), and a maximum of ripe fruits in March/April (over 91%).

Young seeds seem to be eaten throughout the year except for July and October, but account for only a low percentage (1.0 - 3.4%) of total

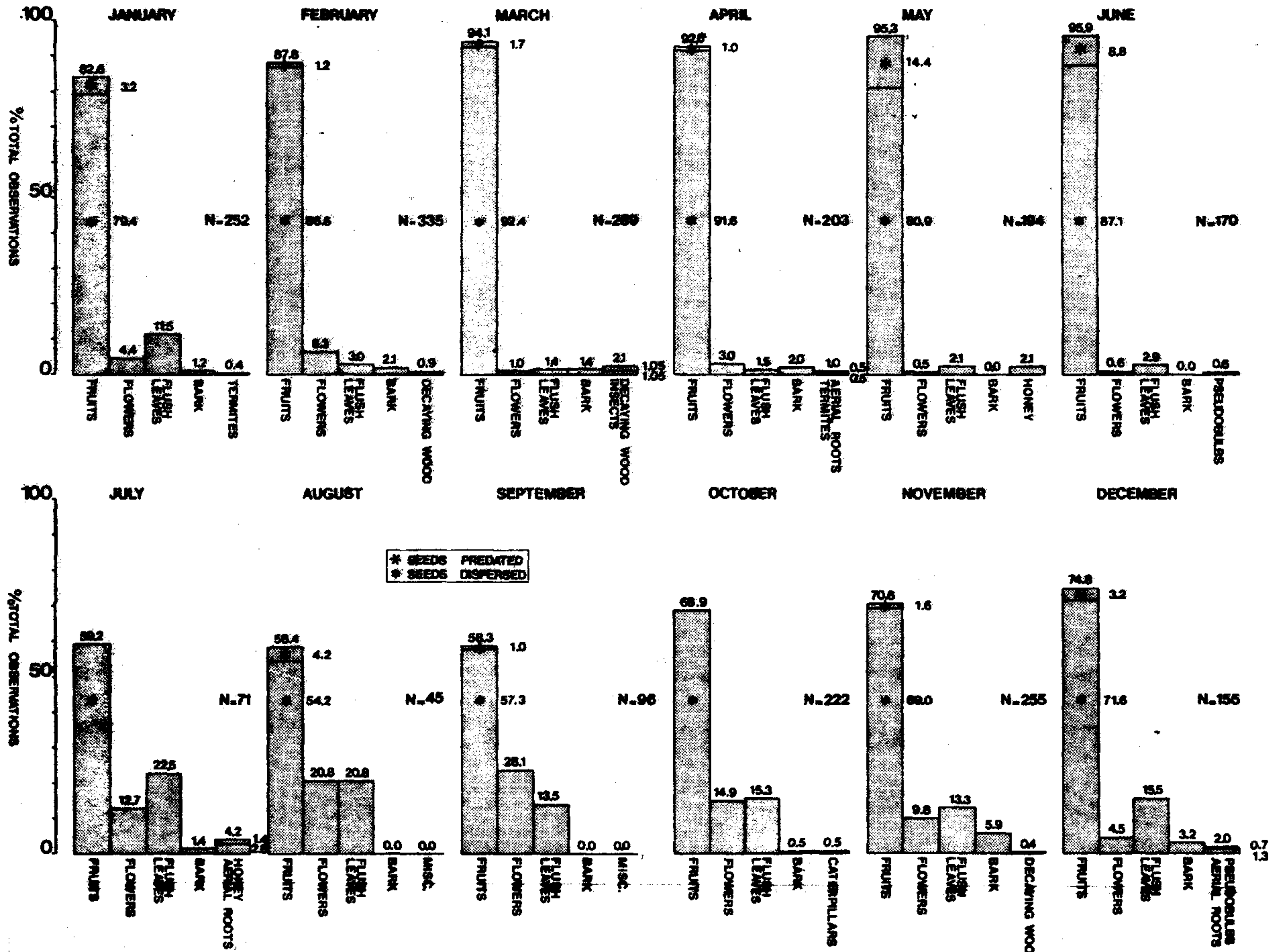


Fig. 10. Monthly variation of food choice in Ateles p. paniscus in the Voltzberg study area, expressed as percentage of the total number of feeding observations for each food category.

feeding records for most months. Relatively high percentages of feeding on young seeds are found in May (14.4%) and June (8.8%), around the peak of the long wet season. By ingesting many young seeds, rich in protein and fat, in this period the monkeys seem to stock up on energy for the coming months of scarcity. Also, this fits the assertion of Amerindians and Bushnegroes in Surinam that the monkeys are heaviest in this time of the year and, consequently, are preferred to be hunted by then.

Flowers. Flowers are eaten throughout the year, but account for only a very low percentage (0.5 - 3.0%) of total feeding records during the long wet season (March - July). The availability of edible flowers is very low too at this time of year (Fig. 9). Flowers, however, account for a considerable part of total feeding records (over about 10%) during the long dry season (July - December), with a peak in September (28.1%), the centre of the dry season. A minor peak is reached in February, during the short dry season (6.3%).

Flush leaves. Flush leaves are eaten throughout the year, but account for only a very low percentage of total feeding records (3% or less) during the months February - July, when they are almost absent (Fig. 9). Flush leaves account for relatively high percentages of total feeding records during the period July - February (over 11.5%), so during the long dry season and the short wet season.

Bark. During the year, spider monkeys were seen feeding on bark only occasionally (0.0-2.1%), except during November and December. In November, feeding on bark accounts for 5.9% of total feeding records, in December for 3.2%. Except in July, bark eating was not observed during the period May - October.

Decaying wood. Decaying wood was seen eaten only during the months February, March and November, but at very low frequencies. In February/March, it accounts for about 1% of total feeding records, in November for 0.4%.

Aerial roots. Aerial roots were seen eaten only in April, July and December, accounting for 0.5, 2.8 and 1.3%, resp., of the total number of feeding records for each month.

Pseudobulbs. Pseudobulbs were seen eaten only during June and December, making up for 0.6 and 0.7%, resp., of total feeding records.

Honey. Honey was seen eaten only in May and July, making up for 2.1 and 1.4%, resp., of total feeding records.

Insects. Insects appeared to be eaten only during part of the year, particularly in March. Termites were seen eaten during January, March and April, accounting for 0.4, 0.35 and 0.5%, resp., of total feeding records, whereas caterpillars were seen eaten only in March and October, making up for 0.7 and 0.5%, resp., of total feeding records.

As shown in Fig. 11, during the months July, August and September (the period of low fruit supply) the monkey compensates its diet with relatively high percentages of both flowers and flush leaves, whereas the percentages appear to be strongly determined individually by its abundance caused by the ecological change (Fig. 9). When fruit abundance is highest (during the months March, April, May and June), both flowers and flush leaves play a minor role in the monkey's diet.

Monthly diet. The monthly diet of Ateles p. paniscus in the Voltzberg study area is visualized graphically in Figs. 12 - 23, showing all food items ranked according to the total number of feeding records for each.

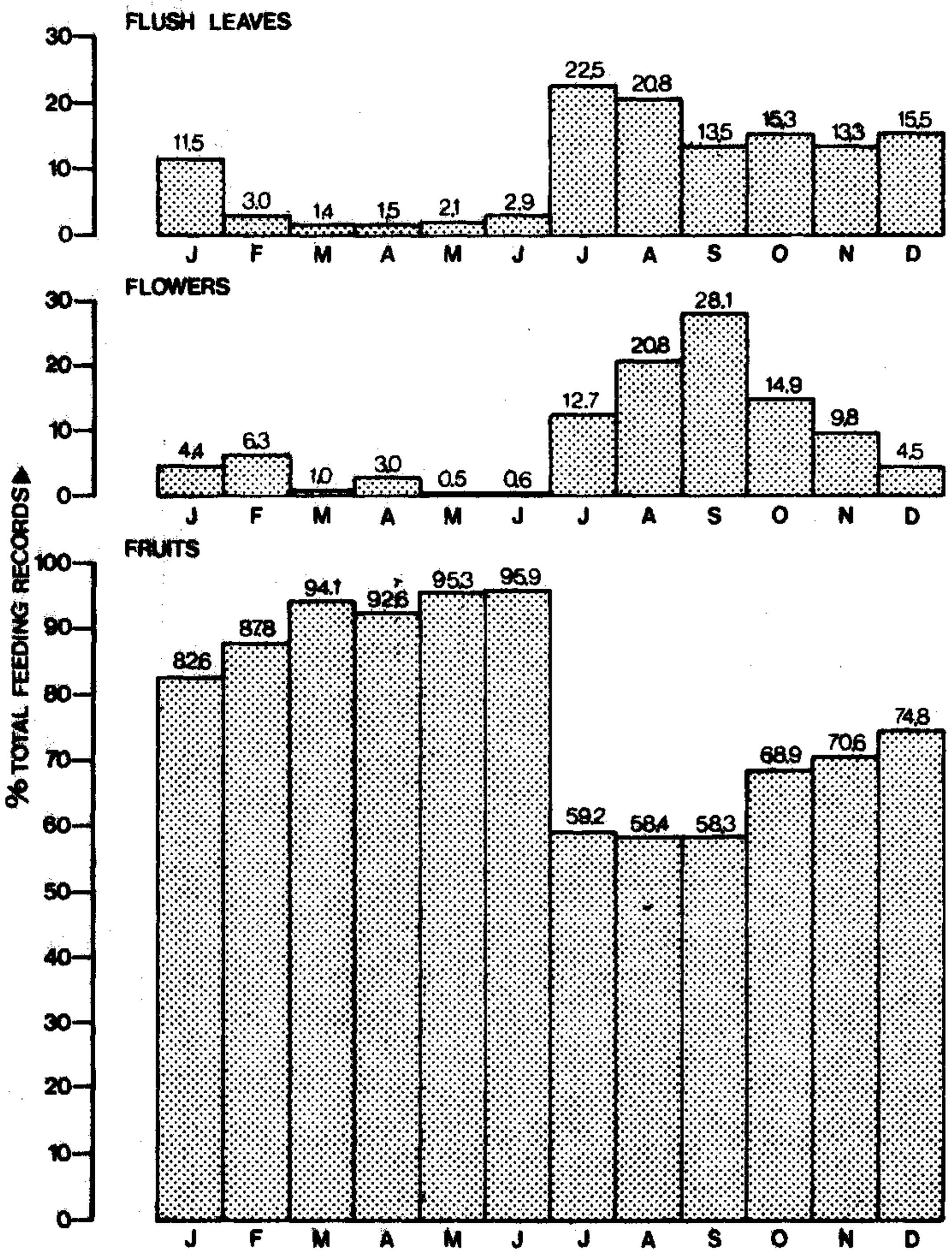


Fig. 11. Monthly percentage of the total number of feeding records compared for flush leaves, flowers and fruits, eaten by *Ateles p. paniscus* in the Voltzberg study area during the present study.

Besides this, the plant part actually eaten is mentioned. Usually, the seeds or stones are drawn too, in particular when dispersed by the monkey. The drawings show monthly diversity of food choice, whereas the relative importance for each food item in a particular month is given by the number of feeding records and its location in the drawing.

4.2.3. Food eaten and food availability. Table 8 compares the monthly availability of food items with the food choice observed. The data derived from Table 1 and Figs. 12 - 23. Food items not included are bark, decaying wood, pseudobulbs, honey and insects because their availability seems to be either permanent (e.g., bark) or hard to determine (e.g., honey).

During the end of the long wet season (June, July) and the first part of the long dry season (August, September), when food supply is lowest, the monkeys seem to exploit all available food sources. In contrast, in particular during December and January, a food excess seems to exist with high percentages of food items not exploited (17.3 and 15% resp.). The foods neglected during December were mainly young seeds and flowers, during January young seeds and several fruits of minor overall importance. However, comparing food availability and food choice in this way, considering all food items equally preferred, doesn't say anything about the real food excess in terms of amounts of foods preferred. Spider monkeys, above all, do prefer ripe fruits. During December and January, months providing them with an excess of food items, the supply of preferred ripe fruits is still rather poor, forcing the monkey to eat considerable amounts of young leaves and flowers.

In contrast, during March, May and June, and particularly during April, the most important food species obviously provide the monkeys with an excess of ripe fruits, resulting in enormous amounts of spontaneously fallen fruits not exploited by them, like when *Guarea grandifolia*, *Tetragastris* spp., *Protium* spp., *Capparis maroniensis*, *Spondias mombin* or *Virola melinonii* are cropping well.

Table 8. Food availability compared with food choice for each month of the year, expressed as the total number of food items. The food excess is expressed as the percentage of food items not exploited. Not included are bark, decaying wood, pseudobulbs, honey and insects

Month	Total number of food items		% Food items not exploited
	available	eaten	
January	53	45	15.0
February	47	42	10.6
March	49	48	2.0
April	54	51	5.6
May	51	47	7.8
June	32	32	0.0
July	31	31	0.0
August	24	24	0.0
September	39	38	2.6
October	50	46	8.0
November	66	60	9.9
December	52	43	17.3


JANUARY
0
5
10cm
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25+42
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
43
44
45
46
47
48
49
50

Figures 12 - 23. Monthly diet of *Ateles p. paniscus* in the Voltzberg study area. The species of food plant and other food are ranked according to the total number of feeding records collected for each month (in parentheses). Besides, the part actually eaten is mentioned. When necessary, an explanation of the corresponding drawing of a food item is added.
The drawings show monthly diversity of food choice, whereas the relative importance for a food item in a particular month is given by its location in the drawing. + = occurring in the Raleighvallen study area; ++ = fruiting less than once a year; y. = young; inflor. = inflorescence; infruct. = infructescence

Figure 12. Diet in January

1. *Virola melinonii*, aril (110); a. just dehiscing fruit b. fruit, one valve removed c. seed with aril - 2. *Cecropia sciadophylla*, infruct. (20) 3. *Inga alba*, mesocarp (10) - 4. *Vataireopsis speciosa*, y. leaves (10) - 5. *Philodendron scandens*, y. leaves (9) - 6. *Laetia procera*, aril (8); a. fruit b. dehiscing fruit from above - 7. *Bagassa guianensis*, infruct. (7) - 8. *Cordia lomatoloba*, mesocarp (6) - 9. *Eperua falcata*, y. leaves (4) - 10. *Newtonia suaveolens*, inflor. (4) - 11. *Pourouma mollis*, whole fruit (4); a. infruct. b. fruit - 12. *Brosimum lactescens*, infruct. (= pseudofruit) (3); a. two-seeded infruct. b. three-seeded infruct. c. seed - 13. *Drypetes variabilis*, whole fruit (3); a. fruit b. fruit, the exocarp and mesocarp partly removed to show the stone - 14. *Moutabea guianensis*, mesocarp (3); a. fruit b. fruit from below c. cross section showing the seeds - 15. *Pouteria* sp., mesocarp (3); a. fruit b. seed, lateral views - 16. *Sacoglottis cydonioides*, whole fruit (3); a. fruit b. stone - 17. ++*Capparis maroniensis*, mesocarp (2); a. fruit b. seed - 18. *Carapa procera*, y. seeds (2); a. just dehiscing fruit b. fruit from above c. seed - 19. *Eperua falcata*, flowers (2); a. inflor. b. flower - 20. *Eschweilera corrugata*, y. seeds (2); a. fruit b. fruit obliquely from below - 21. *Hyeronima laxiflora*, whole fruit (2); part of infruct. - 22. *Hylocereus* sp.a., flowers, esp. tips of stamens and style, and stigma (2) - 23. *Hymenolobium petraeum*, y. leaves (2) - 24. *Inga acrocephala*, mesocarp (2) - 25. *Licania micrantha*, bark (2) - 26. *Pereskia aculeata*, whole fruit (2) - 27. *Philodendron acutatum*, infruct. (2); part of infruct., most of the fruits eaten by the monkey - 28. *Bellucia grossularioides*, whole fruit (1); a. fruit b. fruit from above - 29. *Campomanesia aromatica*, whole fruit (1) - 30. *Carapa procera*, flowers (1); a. flower b. flower from above - 31. *Carapa procera*, y. leaves + base of petiole (1) - 32. *Cedrelinga cateniformis*, y. seeds (1); part of young pod showing two seeds - 33. *Clusia grandiflora*, pulp (= arils of many seedlets) (1) - 34. *Combretum rotundifolium*, y. seeds (1); a. fruit b. fruit from above - 35. *Copaifera guianensis*, aril (1); a. fruit b. seed - 36. *Dioclea macrocarpa*, y. seeds (1); a. pod b. seed - 37. *Enterolobium schomburgkii*, inflor. (1) - 38. *Eperua rubiginosa*, y. seeds, esp. plumula (1); pod, one valve removed, showing the seeds - 39. *Ephedranthus guianensis*, mesocarp (1); a. infruct. b. seed - 40. +*Eugenia* sp., whole fruit (1); a. infruct. b. seed - 41. *Gnetum urens*, perigonium or whole fruit (1); a. infruct. b. seed - 42. *Inga alba*, bark (1) - 43. *Inga thibaudiana*, mesocarp (1) - 44. *Jacaratia spinosa*, y. leaves - 45. *Malmea obovata*, whole fruit (1); a. part of infruct. b. seed - 46. *Norantea guianensis*, flowers, esp. the honeycups (1); part of inflor. - 47. *Peperomia glabella*, y. leaves (1) - 48. *Strychnos tomentosa* , mesocarp (1); a. fruit b. seed, lateral views - 49. *Tabebuia serratifolia*, y. leaves (1) - 50. *Termites*, whole insects (1)

In total: 50 food items
45 food plant species 252 feeding records
1 insect species

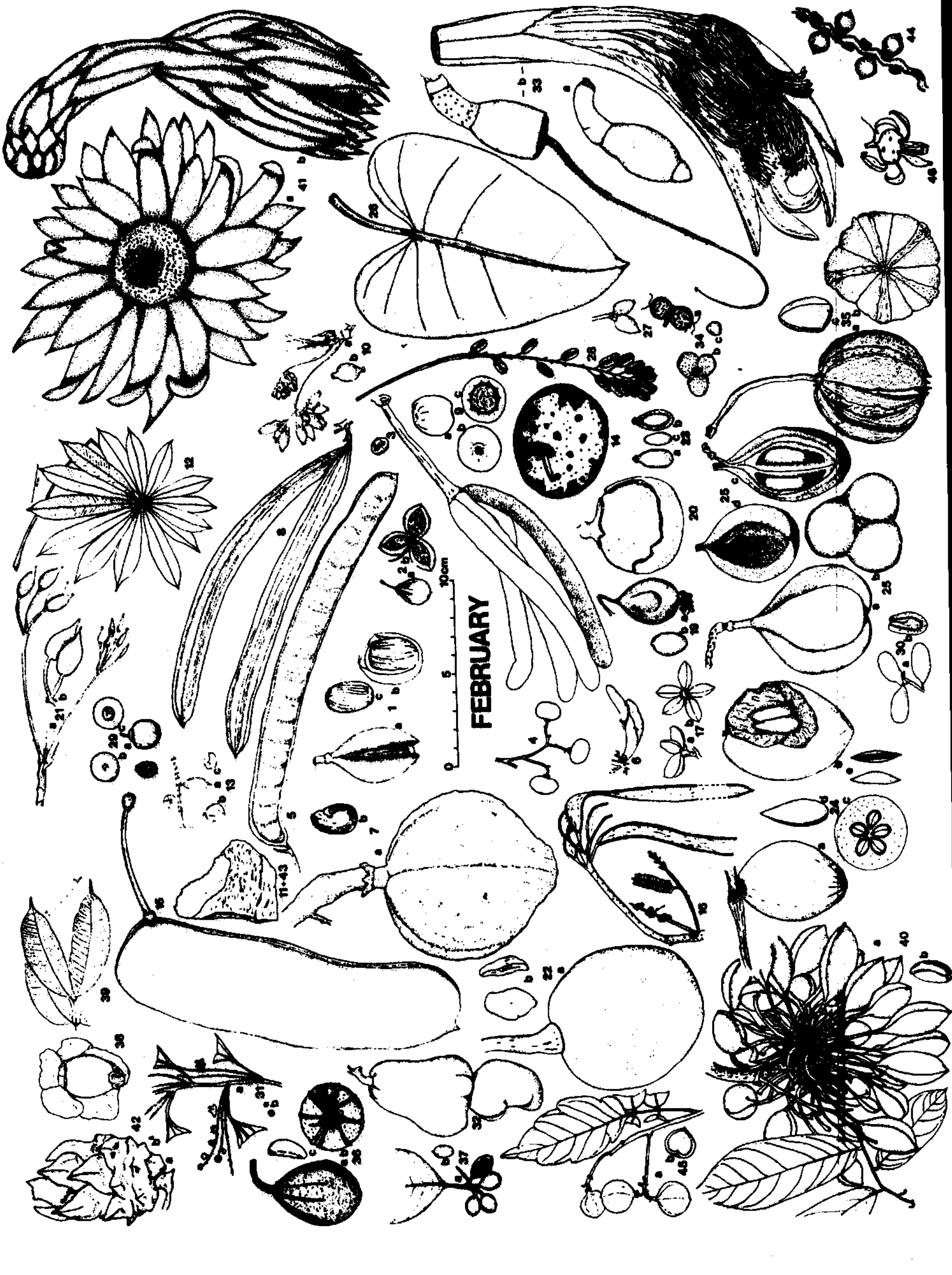

FEBRUARY
0
5
10cm
1
2
4
5
6
7
8
10
11-43
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
44
45
46

Figure 13. Diet in February

1. *Virola melinonii*, aril (105); a. just dehiscing fruit b. fruit, one valve removed c. seed with aril - 2. *Laetia procera*, pulp (= arils of many seedlets) (32); a. fruit b. dehiscing fruit from above - 3. *Cecropia sciadophylla*, infruct. (25) - 4. *Cordia lomatoloba*, mesocarp (22) - 5. *Inga alba*, mesocarp (21) - 6. *Norantea guianensis*, flowers, esp. the honeycups (15); part of inflor. - 7. ++*Capparis maroniensis*, mesocarp (12) a. fruit b. seed - 8. *Inga edulis*, mesocarp (9) - 9. *Ampelocera edentula*, mesocarp (8); a. fruit b. fruit from below c. cross section, showing one stone - 10. *Pourouma mollis*, whole fruit (7); a. infruct. b. fruit - 11. *Licania micrantha*, bark (6) - 12. *Cecropia sciadophylla*, y. leaves (5) - 13. *Paullinia acuminata*, aril (5); a. infruct. b. other type of fruit c. seed with aril - 14. *Bagassa guianensis*, infruct. (4) - 15. *Inga acrocephala*, mesocarp (4) - 16. *Newtonia suaveolens*, inflor. (4) - 17. *Quassia simarouba*, mesocarp (4); a. fruit b. fruit from above - 18. *Attalea speciosa*, decaying and rotten sheaths of long before shed leaves (3) 19. *Cayaponia ophthalmica*, mesocarp (3); a. fruit b. seed - 20. *Licania majuscula*, exocarp + mesocarp (3); fruit, the outer layer partly scraped off by the monkey, showing the big stone - 21. *Pourouma minor*, whole fruit (3); a. young infruct. b. mature fruits - 22. *Strychnos tomentosa*, mesocarp (3); a. fruit b. seed, lateral views - 23. *Trichilia quadrijuga*, aril (3); a. fruit b. longitudinal section c. seed - 24. *Ecclinusa* sp., y. seeds and mesocarp (2); a. fruit b. fruit partly opened by the monkey, showing some young seeds c. cross section d.,e. seed, lateral views - 25. *Paullinia spicata*, aril (2); a. fruit b. fruit from above c. fruit, one valve removed d. valve from inside - 26. *Philodendron scandens*, y. leaves (2) - 27. *Pourouma* sp., whole fruit (2); part of infruct. - 28. *Vataireopsis speciosa*, y. leaves (2) - 29. *Vitex stahelii*, whole fruit or mesocarp only (2); a. fruit b. fruit from above c. fruit from below - 30. *Abuta grandifolia*, mesocarp (1); a. part of infruct. with two types of fruit b. stone - 31. *Alchorneopsis floribunda*, whole fruit (1); a. infruct. b. seed - 32. *Anacardium giganteum*, pseudofruit (= pedicel) (1) - 33. *Bombax spectabile*, flowers + floral buds (1); a. floral bud b. flower - 34. *Brosimum lactescens*, infruct. (1); a. two-seeded b. three-seeded infruct. c. seed - 35. *Carapa procera*, y. seeds (1); a. just dehiscing fruit b. fruit from above c. seed - 36. +*Cheiloclinium* cf. *gleasonianum*, mesocarp (1); a. fruit b. fruit from below c. seed - 37. *Chrysophyllum auratum*, mesocarp (1); a. infruct. b. seed - 38. *Clusia scrobiculata*, pulp (= arils of many seedlets) (1) - 39. *Eperua falcata*, y. leaves (1) - 40. *Ephedranthus guianensis*, mesocarp (1); a. infruct. b. seed - 41. *Hylocereus* sp. a., flowers, esp. tips of stamens and style, and stigma (1); a. flower from above b. flower, lateral view - 42. *Hylocereus* sp. b., whole fruit (1); a. fruit b. seed - 43. *Inga alba*, bark (1) - 44. *Oenocarpus bacaba*, whole fruit (1); part of infruct. - 45. *Paullinia sphaerocarpa*, y. seeds + aril (1); a. infruct. b. valve from inside 46. *Pereskia aculeata*, whole fruit (1)

In total: 46 food items   335 feeding records
44 food plant species

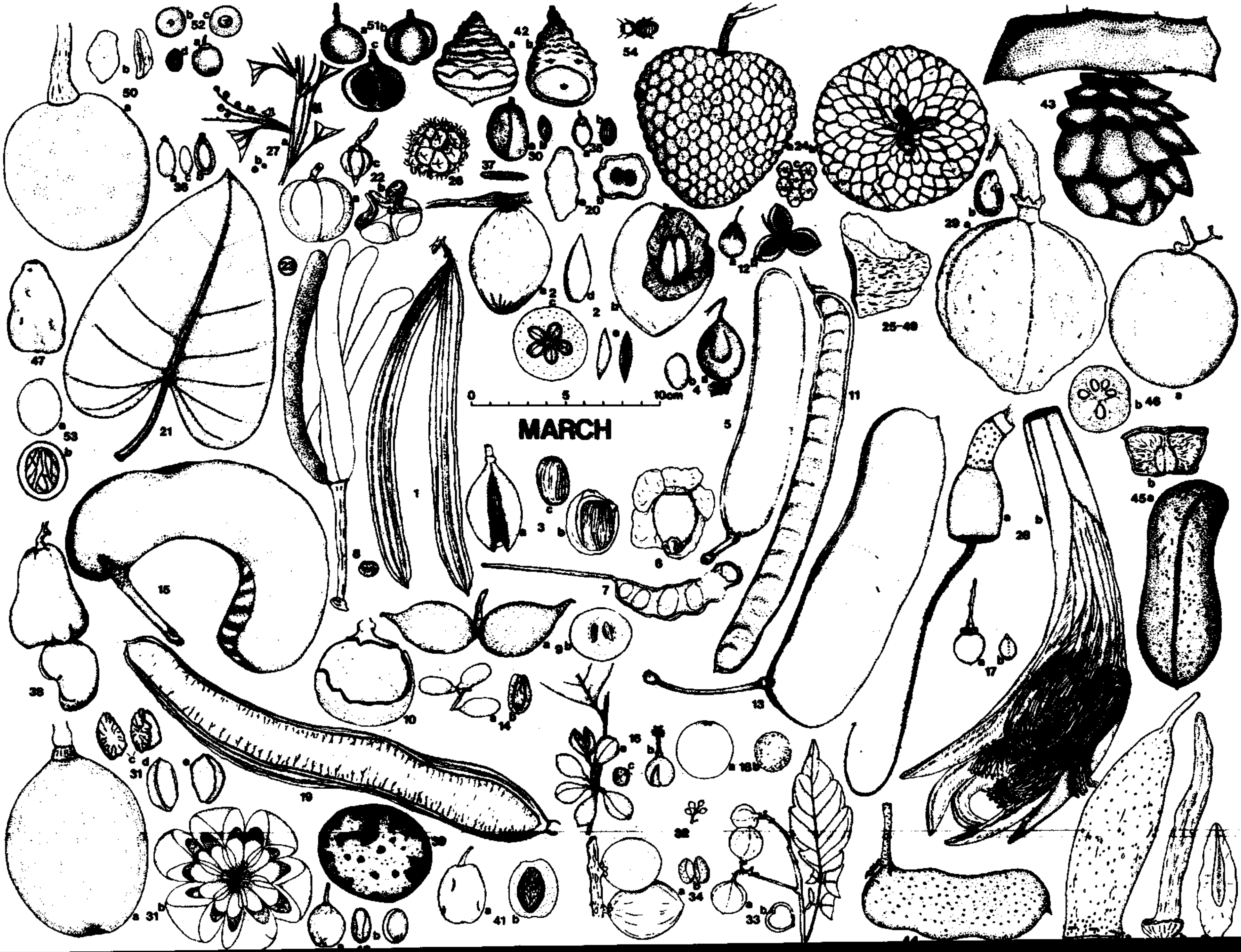

MARCH
0
5
10cm
1
2
3
4
5
6
7
9
10
11
12
13
14
15
17
19
20
21
22
24
25-40
26
27
28
29
30
31
33
34
35
36
37
38
41
42
43
45
46
47
50
51
52
53
54

Figure 14. Diet in March

1. Inga edulis, mesocarp (44) - 2. Ecclinusa sp., mesocarp (38); a. fruit b. fruit partly opened by the monkey, showing some seeds c. cross section d., e. seed, lateral views - 3. Virola melinonii, aril (24); a. just dehiscing fruit b. fruit, one valve removed c. seed with aril - 4. Cayaponia ophthalmica, mesocarp (14); a. fruit b. seed - 5. Inga bourgoni, mesocarp (13) - 6. Clusia scrobiculata, pulp (= arils of many seedlets) (10) - 7. Inga leiocalycina, mesocarp (9) - 8. Cecropia sciadophylla, infruct. (8) - 9. Geissospermum sp., juice (8); a. fruit b. cross section 10. Licania majuscula, exocarp + mesocarp (8); fruit, the outer layer partly scraped off by the monkey, showing the big stone - 11. Inga alba, mesocarp (7) - 12. Laetia procera, pulp (= arils of many seedlets (7); a. fruit b. dehiscing fruit from above - 13. Inga acrocephala, mesocarp (6) - 14. Abuta grandifolia, mesocarp (5); a. part of infruct. with two types of fruit b. stone - 15. Inga acreana, mesocarp (5); dehiscing fruit 16. Maytenus sp., aril (5); a. infruct. b. dehiscing fruit c. seed - 17. Ocotea wachenheimii, whole fruit (5); a. fruit b. seed - 18. Sacoglottis cydonioides, whole fruit (5); a. fruit b. stone - 19. Inga rubiginosa, mesocarp (4) - 20. Parinari excelsa, exocarp + mesocarp (4); a. fruit b. cross section - 21. Philodendron scandens, y. leaves (4) - 22. Tetragastris panamensis, mesocarp (4); a. fruit b. fruit from below, the valves removed and three stones with mesocarp eaten out c. lateral view, all valves removed - 23. Attalea speciosa, decaying and rotten sheaths of long before shed leaves (3) - 24. Duguetia sp., infruct. (3); a. infruct. b. infruct. from below c. several fruitlets from above - 25. Inga alba, bark (3) - 26. Perebea mollis, infruct. (3); infruct. from above - 27. Alchorneopsis floribunda, whole fruit (2); a. infruct. b. seed - 28. Bombax spectabile, flowers (2); a+b. flower - ++29. Capparis maroniensis, mesocarp (2); a. fruit b. seed - 30. Cheiloclinium sp. (249), mesocarp (2); a. fruit b. seed - 31. Guarea grandifolia, aril (2); a. fruit b. dehiscing fruit from above c. stone without aril, lateral views d+e. stone with aril, lateral views - 32. Hyeronima laxiflora, whole fruit (2); part of infruct. - 33. Paullinia sphaerocarpa, aril (2); a. infruct. b. valve from inside - 34. Pouteria guianensis, mesocarp (2); a. fruits b. seed, lateral views - 35. Styrax cf. fanshawei, whole fruit or mesocarp (2); a. fruit b. seed - 36. Trichilia quadrijuga, aril or whole fruit (2); a. fruit b. fruit, one valve removed c. seed - 37. Caterpillars (2) - 38. Anacardium giganteum, pseudofruit (= pedicel) (1) - 39. Bagassa guianensis, infruct. (1) - 40. Couratari guianensis, y. seeds (1); a. fruit without operculum b. columella with operculum c. seed - 41. Drypetes variabilis, whole fruit (1); a. fruit b. fruit, the exocarp and mesocarp partly removed to show the stone - 42. Eschweilera corrugata, y. seeds (1); a. fruit b. fruit obliquely from below - 43. Hylocereus sp. a., whole fruit (1) - 44. Inga cf. capitata, mesocarp (1) - 45. Tanaecium jaroba, y. seeds (1); a. fruit b. seed - +46. Parahancornia amapa, mesocarp (1); a. fruit b. cross section, showing the seeds - 47. Parinari campestris, exocarp + mesocarp (1) - 48. Pouteria sp., mesocarp (1); a. fruit b. seed, lateral views - 49. Sacoglottis cydonioides, bark (1) - 50. Strychnos tomentosa, mesocarp (1); a. fruit b. seed, lateral views - 51. Tetragastris altissima, mesocarp (1); a. one-seeded fruit b. more-seeded fruit c. fruit, two valves removed - 52. Vitex stahelii, whole fruit or mesocarp only (1); a. fruit b. fruit from above c. fruit from below d. stone - 53. Not identified species (1); a. fruit b. fruit, exocarp and mesocarp partly removed, showing the stone - 54. Termites, whole insects (1)

In total: 54 food items
50 food plant species   289 feeding records
2 insect species

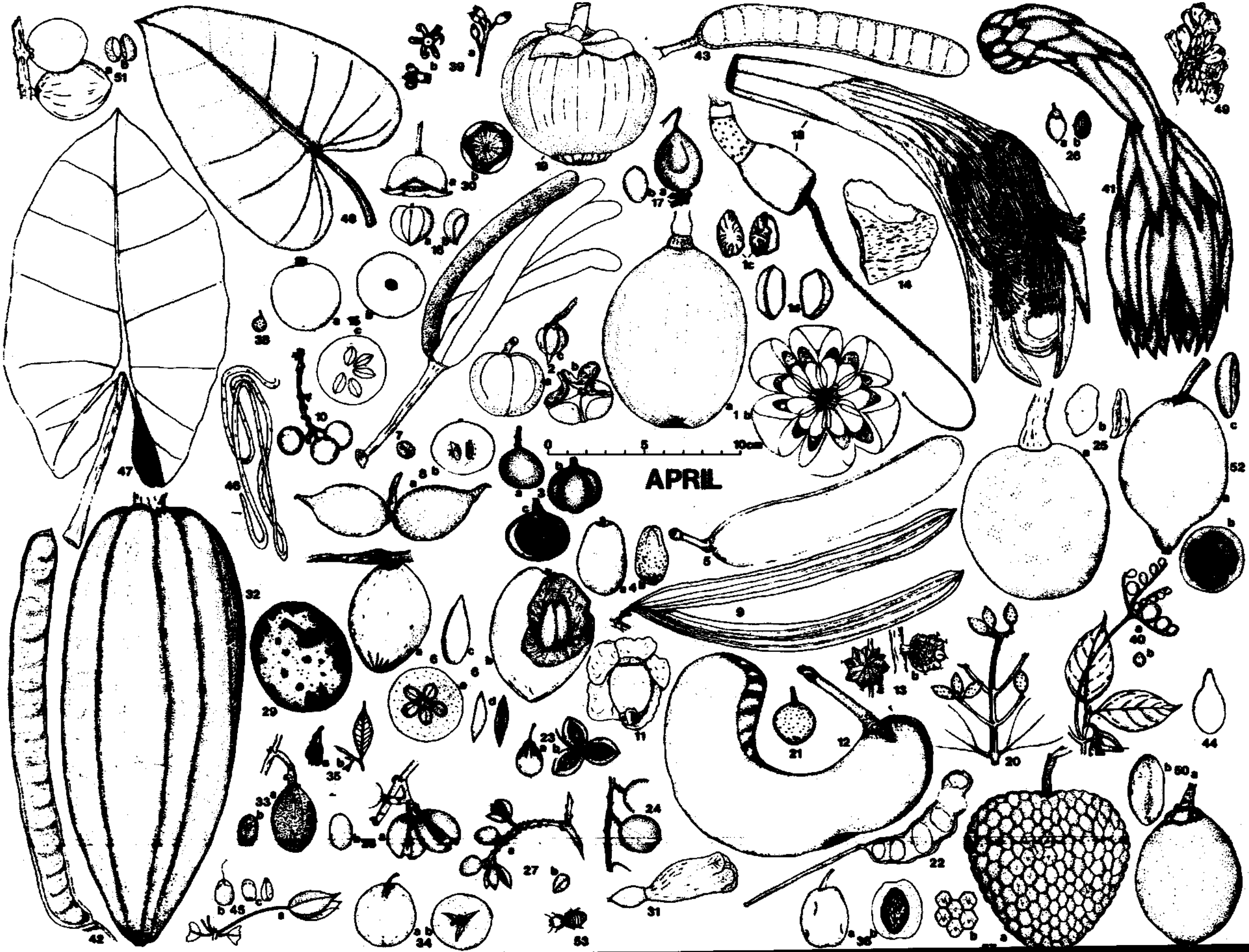

51
39
19
43
49
26
41
48
30
17
18
16
1c
1d
14
38
15
2
1
10
7
47
46
3
0
5
10cm
APRIL
25
52
5
4
8
9
32
29
6
13
40
11
23
21
12
20
44
35
33
28
27
24
22
50
45
31
36
42
34
53

Figure 15. Diet in April

1. Guarea grandifolia, aril (35); a. fruit b. dehiscing fruit from above c. stone without aril, lateral views d. stone with aril, lateral views - 2. Tetragastris panamensis, mesocarp (19); a. fruit b. fruit from below, the valves removed and three stones with mesocarp eaten out c. lateral view, all valves removed - 3. Tetragastris altissima, mesocarp (14); a. one-seeded fruit b. more-seeded fruit c. fruit, two valves removed - 4. Spondias mombin, mesocarp (12); a. fruit b. stone - 5. Inga bourgoni, mesocarp (10) - 6. Ecclinusa sp., mesocarp (8); a. fruit b. fruit, partly opened by the monkey, showing some seeds c+d. seed, lateral views e. cross section - 7. Cecropia sciadophylla, infruct. (7) - 8. Geissospermum sp., juice (7); a. fruit b. cross section - 9. Inga edulis, mesocarp (7) 10. Cayaponia rigida, whole fruit (6); infruct. - 11. Clusia scrobiculata, pulp (= arils of many seedlets) (6) - 12. Inga acreana, mesocarp (5) - 13. Helicostylis tomentosa, infruct. (4); a. infruct. from above b. infruct. obliquely from below - 14. Inga alba, bark (4) - 15. Moutabea guianensis, mesocarp (4); a. fruit b. fruit from below c. cross section showing the seeds - 16. Protium neglectum, mesocarp (4); a. more-seeded fruit b. one-seeded fruit - 17. Cayaponia ophthalmica, mesocarp (3); a. fruit b. seed - 18. Bombax spectabile, flowers (2) - 19. Clusia grandiflora, pulp (= arils of many seedlets) (2) - 20. Coussarea paniculata, whole fruit (2); infruct. - 21. Ficus trigonata, whole figs (2) - 22. Inga leiocalycina, mesocarp (2) - 23. Laetia procera, pulp (= arils of many seedlets) (2); a. fruit b. dehiscing fruit from above - 24. Protium polybotryum, mesocarp (2); part of infruct. - 25. Strychnos tomentosa, mesocarp (2); a. fruit b. seed, lateral views - 26. Styrax cf. fanshawei, whole fruit or mesocarp only (2); a. fruit b. seed - 27. Trichilia martiana, aril or whole fruit (2); a. infruct. b. seed - 28. Virola surinamensis, aril (2); a. part of infruct. with dehiscing fruits b. seed - 29. Bagassa guianensis, infruct. (1) - 30. Bellucia grossularioides, whole fruit (1); a. fruit b. fruit from above - 31. Species c. (Bignoniaceae), flowers (1) - 32. Bombax spectabile, y. seeds (1); young fruit - 33. Cheiloclinium cognatum, (young) seeds (1); a. fruit b. seed - 34. Cheiloclinium sp. (3549), mesocarp (1); a. fruit b. fruit from below - 35. Cynometra marginata, y. leaves (1); a. leaf bud b. y. leaf - 36. Drypetes variabilis, whole fruit (1); a. fruit b. fruit, exocarp and mesocarp partly removed to show the stone - 37. Duguetia sp., infruct. (1); a. infruct. b. several fruitlets from above - 38. Ficus pertusa, whole figs (1) - 39. Guarea grandifolia, flowers (1); a. part of inflor. with floral buds b. flower - 40. Guettarda acreana, whole fruit (1); a. infruct. b. seed - 41. Hylocereus sp. a., flowers, esp. tips of stamens and style, and stigma (1) - 42. Inga alba, mesocarp (1) - 43. Inga stipularis, mesocarp (1) - 44. Licania densiflora, exocarp + mesocarp (1) - 45. Mendoncia hoffmannseggiana, mesocarp (1); a. fruit b. fruit, the bracts removed c. stone - 46. Philodendron acutatum, tips and epiderm of aerial roots (1); part of aerial root - 47. Philodendron acutatum, y. leaves (1) - 48. Philodendron scandens, y. leaves (1) - 49. Philodendron sp., infruct. (1); part of infruct., several fruitlets eaten off - 50. Platonia insignis, aril (1); a. fruit b. seed - 51. Pouteria guianensis, mesocarp (1); a. fruits b. seed, lateral views - 52. Rheedia macrophylla, aril (1); a. fruit b. cross section c. seed - 53. Termites, whole insects (1)

In total: 53 food items
48 food plant species   203 feeding records
1 insect species

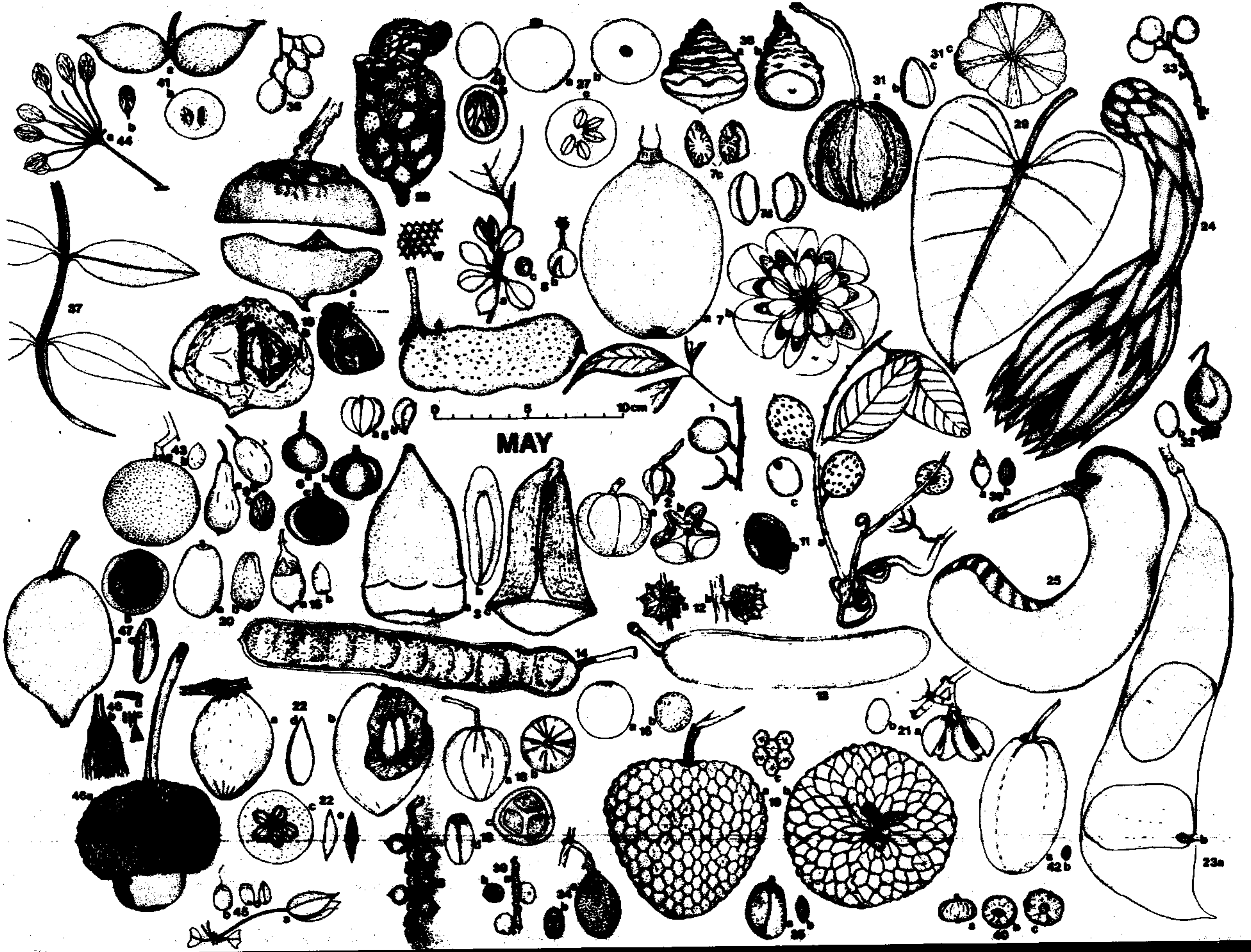

MAY
0
5
10cm
44
41
36
37
27
38
31
29
33
24
7c
7a
7
1
32
39
43
5
2
11
3
12
25
47
20
15
14
13
46
22
18
16
21
42
23a
46a
45
30
34
35
40

Figure 16. Diet in May

1. *Protium polybotryum*, mesocarp (24) - 2. *Tetragastris panamensis*, mesocarp (21); a. fruit b. fruit from below, the valves removed and three stones with mesocarp eaten out c. lateral view, all valves removed - 3. *Couratari stellata*, young seeds + base of columella (13); a. fruit b. seed c. columella + operculum - 4. *Inga* cf. *capitata*, mesocarp (11) - 5. *Protium neglectum*, mesocarp (11); a. more-seeded fruit b. one-seeded fruit - 6. *Tetragastris altissima*, mesocarp (9); a. one-seeded fruit b. more-seeded fruit c. fruit, two valves removed - 7. *Guarea grandifolia*, aril (8); a. fruit b. dehiscing fruit from above c. stone without aril, lateral views d. stone with aril, lateral views - 8. *Maytenus* sp., aril (8); a. infruct. b. dehiscing fruit c. seed - 9. *Clarisia racemosa*, whole fruit (6); a+b. two types of fruit c. seed - 10. *Eschweilera poiteaui*, y. seeds + aril (6); a. fruit opened, the seeds removed b. fruit, partly opened by the monkey, showing one seed c. seed with aril - 11. *Dicranostyles guianensis*, mesocarp (5); a. infruct. b. one valve from inside c. seed - 12. *Helicostylis tomentosa*, infruct. (5); a. infruct. from above b. infruct. obliquely from below - 13. *Inga bourgoni*, mesocarp (4) - 14. *Inga pezizifera*, mesocarp (4) - 15. *Maripa scandens*, y. seeds (4); a. fruit b. seed - 16. *Sacoglottis cydonioides*, whole fruit (4); a. fruit b. stone - 17. *Honey* (4) - 18. *Cheiloclinium podostemum*, mesocarp (3); a. fruit b. fruit from below c. cross section, showing the seeds d. seed - 19. *Duguetia* sp., infruct. (3); a. infruct. b. infruct. from below c. several fruitlets from above - 20. *Spondias mombin*, mesocarp (3); a. fruit b. stone - 21. *Virola surinamensis*, aril (3); a. dehiscing fruits b. seed, the aril removed - 22. *Ecclinusa* sp., mesocarp (2); a. fruit b. fruit, partly opened by the monkey, showing some seeds c. cross section d+e. seed, lateral views - 23. *Eperua falcata*, y. seeds esp. the plumula (2); a. fruit, one valve removed b. plumula - 24. *Hylocereus* sp. a., flower, esp. tips of stamens and style, and stigma - 25. *Inga acreana*, mesocarp (2); dehiscing pod - 26. *Monstera adansonii*, infruct.(2); infruct.,several fruits at the base eaten by the monkey - 27. *Moutabea guianensis*, mesocarp (2); a. fruit b. fruit from below c. cross section, showing the seeds - 28. *Oenocarpus bacaba*, whole fruit (2); part of infruct. - 29. *Philodendron scandens*, y. leaves (2) - 30. *Styrax* cf. *fanshawei*, whole fruit or mesocarp (2); a. fruit b. seed - 31.*Carapa procera*, y. seeds (1); a. dehiscing fruit b. y. seed c. fruit from above - 32. *Cayaponia ophthalmica*, mesocarp (1); a. fruit b. seed - 33. *Cayaponia rigida*, whole fruit (1); infruct. - 34. *Cheiloclinium cognatum*, (young) seeds (1); a. fruit b. seed - 35. *Cheiloclinium* sp. (249), mesocarp (1); a. fruit b. seed - 36. *Dialium guianense*, aril (1); part of infruct. - 37. *Dipteryx odorata*, y. leaves (1) - 38. *Eschweilera corrugata*, y. seeds + aril (1); a. fruit b. fruit obliquely from below - 39. *Euterpe oleracea*, whole fruit (1); a. part of infruct. b. stone - 40. *Ficus gomelleira*, whole fig (1); a. fig, lateral view b. fig from below c. fig from above - 41. *Geissospermum* sp., juice (1); a. fruit b. cross section - 42. *Jacaratia spinosa*, whole fruit (1); a. fruit b. seed - 43. *Leonia glycycarpa*, mesocarp (1); a. fruit b. seed - 44. *Malmea obovata*, whole fruit (1); a. infruct. b. seed - 45. *Mendoncia hoffmannseggiana*, mesocarp (1); a. fruit b. fruit, the bracts removed c. stone, lateral views - 46. *Parkia nitida*, inflor., esp. the stamens and styles of the fertile flowers at the top (1); a. inflor. b. sterile flowers c. fertile flowers d. leaflet - 47. *Rheedia macrophylla*, aril (1); a. fruit b. cross section showing the seeds c. seed - 48. *Not identified species*, (1); a. fruit b. fruit, the exocarp and mesocarp partly removed, showing the big stone

In total: 48 food items
47 food plant species　　194 feeding records
1 honey

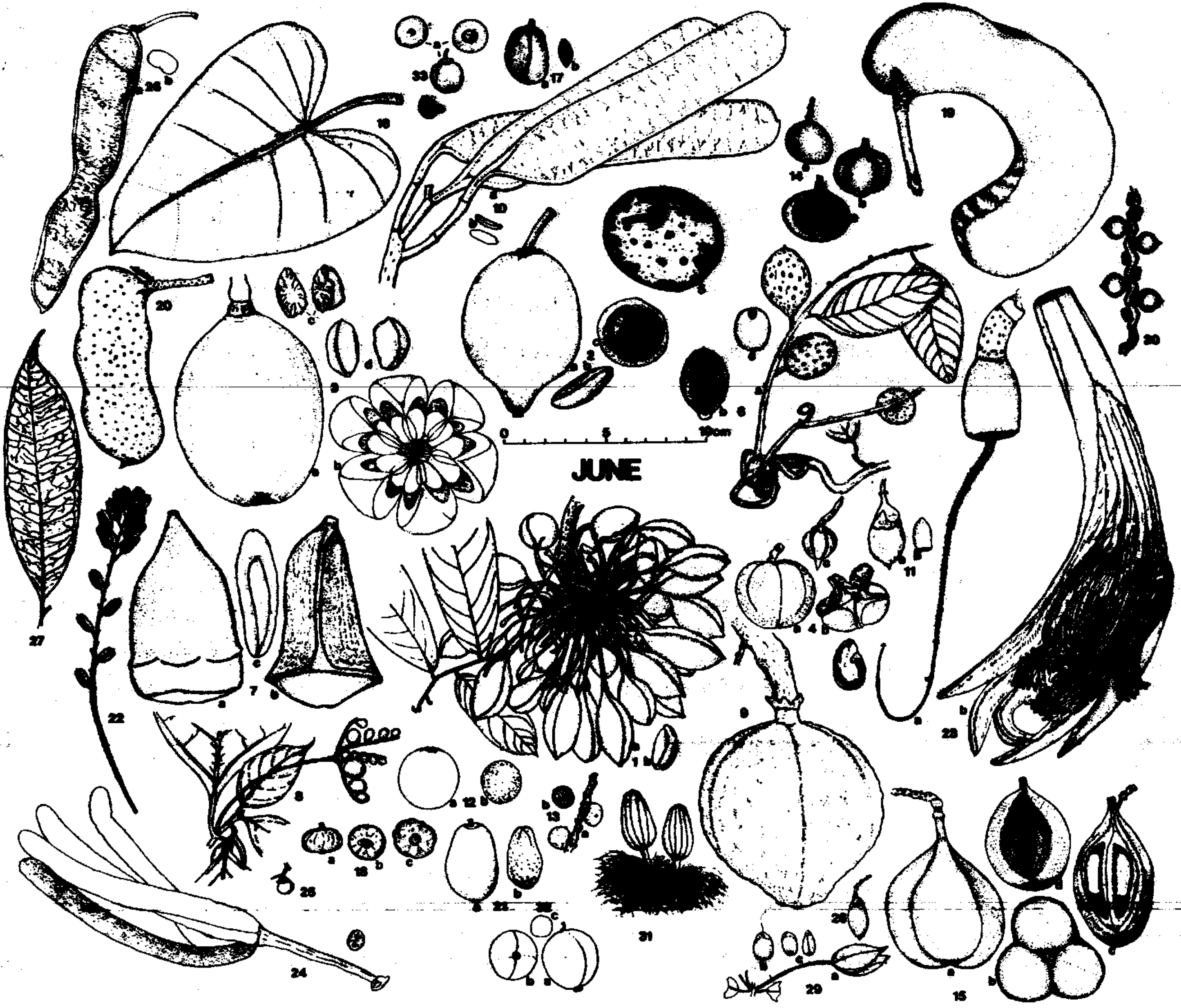

0
5
10cm
JUNE

Figure 17. Diet in June

1. Ephedranthus guianensis, mesocarp (29); a. infruct. b. seed - 2. Rheedia macrophylla, aril (20); a. fruit b. seed c. cross section, showing the seeds - 3. Guarea grandifolia, aril (17); a. fruit b. dehiscing fruit from above c. stone without aril, lateral views d. stone with aril, lateral views - 4. Tetragastris panamensis, mesocarp (11); a. fruit b. fruit from below, the valves removed and three stones with mesocarp eaten out c. lateral view, all valves removed - 5. Bagassa guianensis, infruct. (10) - 6. Dicranostyles guianensis, mesocarp (10); a. infruct. b. valve from inside c. seed - 7. Couratari stellata, y. seeds + columella (9); a. fruit b. columella + operculum c. seed - 8. Guettarda acreana, whole fruit (7);infruct. - 9. Capparis maroniensis, mesocarp (6); a. fruit b. seed - 10. Dimorphandra multiflora, desiccated mesocarp (5); a. part of infruct. b. seed, lateral views - 11. Maripa scandens, y. seeds (5); a. fruit b. seed - 12. Sacoglottis cydonioides, whole fruit (5); a. fruit b. stone - 13. Euterpe oleracea, whole fruit (4); a. part of infruct. b. stone - 14. Tetragastris altissima, mesocarp (4); a. one-seeded fruit b. more-seeded fruit c. fruit, two valves removed - 15. Paullinia spicata, aril (3); a. fruit b. fruit from above c. fruit, one valve removed, showing the seeds d. valve from inside - 16. Philodendron scandens, y. leaves (3) - 17. Cheiloclinium sp. (249), mesocarp (2); a. fruit b. seed - 18. Ficus gomelleira, whole fig (2); a. fig, lateral view b. fig from below c. fruit from above - 19. Inga acreana, mesocarp (2); dehiscing pod - 20. Inga cf. capitata, mesocarp (2) - 21. Spondias mombin, mesocarp (2); a. fruit b. stone - 22. Vataireopsis speciosa, y. leaves (2) - 23. Bombax spectabile, flowers, esp. the tips of stamens and style (1); a+b. flower - 24. Cecropia surinamensis, infruct. (1) - 25. Cordia panicularis, whole fruit (1) - 26. Inga coriacea, mesocarp (1); a. fruit b. seed - 27. Maquira guianensis, y. leaves (1) - 28. Maripa glabra, y. seeds (1) - 29. Mendoncia hoffmannseggiana, mesocarp (1); a. fruit b. fruit, the bracts removed c. stone, lateral views - 30. Oenocarpus bacaba, whole fruit (1); part of infruct. - 31. Species a. (Orchidaceae), pseudobulbs (1) - 32. Trymatococcus paraensis, whole fruit (1); a. fruit b. fruit from above c. seed - 33. Vitex stahelii, whole fruit or mesocarp (1); a. fruit, different views b. stone

In total:	33 food items	170 feeding records
	33 food plant species	

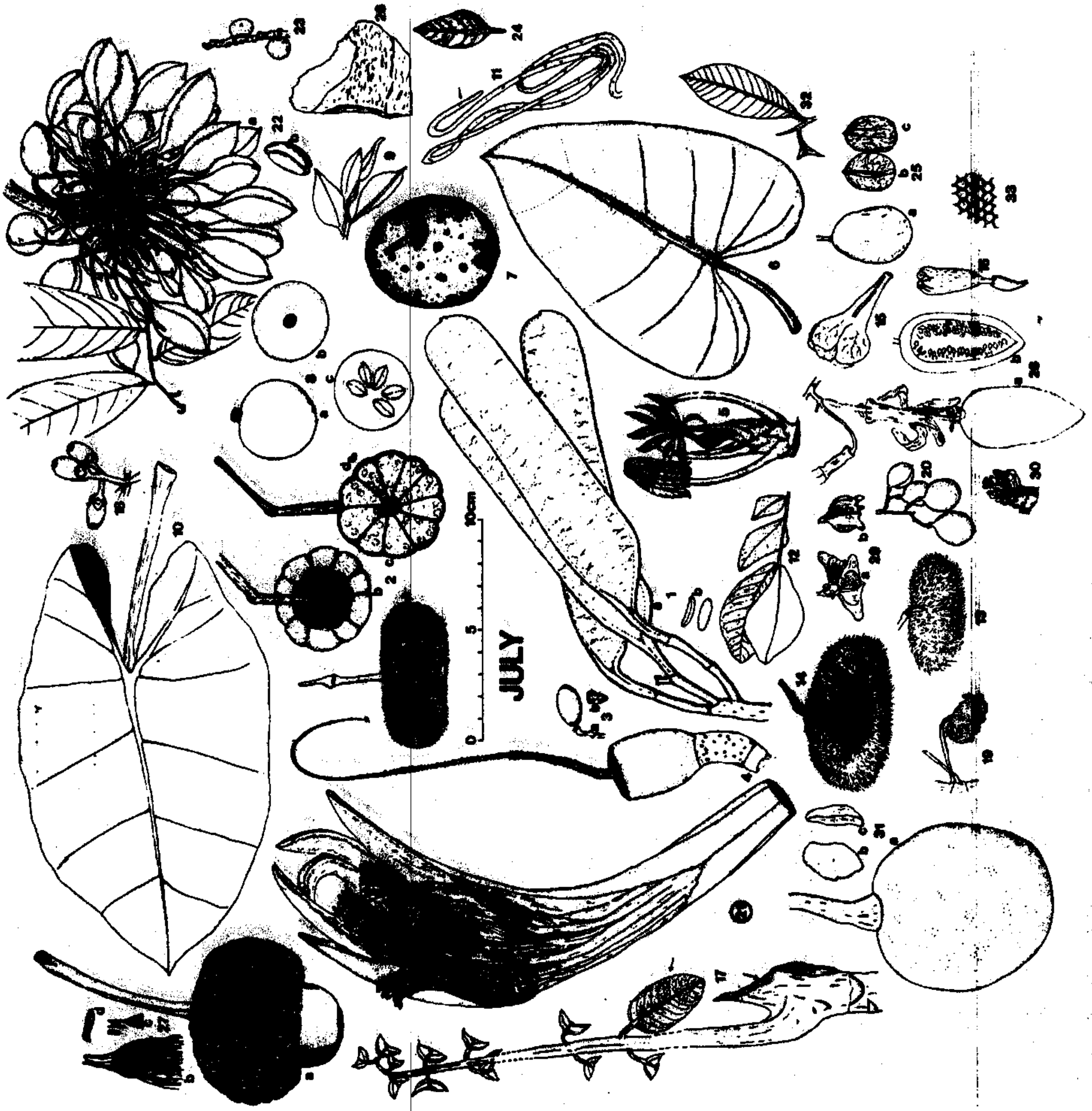

JULY
0
5
10cm
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
a
b
c
d

Figure 18. Diet in July

1. *Dimorphandra multiflora*, desiccated mesocarp (16); a. part of infruct. b. seed, lateral views - 2. *Apeiba echinata*, mesocarp (6); a. fruit b. fruit from below, the exocarp removed c. fruit from above, the exocarp removed d. seed - 3. *Minquartia guianensis*, whole fruit (6); a. fruit b. stone - 4. *Bombax spectabile*, flowers, esp. tips of stamens and style (4); a+b. flower - 5. *Bombax spectabile*, y. leaves (3); part of shoot with y. leaves - 6. *Philodendron scandens*, y. leaves (3) - 7. *Bagassa guianensis*, infruct. (2) - 8. *Moutabea guianensis*, mesocarp (2); a. fruit b. fruit from below c. cross section, showing the seeds - 9. *Peperomia glabella*, y. leaves (2); shoot with y. leaves - 10. *Philodendron acutatum*, y. leaves (2) - 11. *Philodendron scandens*, tips of aerial roots (2) - 12. *Pithecellobium jupunba*, y. leaves (2) - 13. *Apeiba glabra*, mesocarp (1); fruit 14. *Apeiba schomburgkii*, mesocarp (1); fruit - 15. *Species a.* (Bignoniaceae), flowers (1); corolla - 16. *Species b.* (Bignoniaceae), flowers (1); flower - 17. *Carapa procera*, y. leaves + base of petiole (1) - 18. *Clusia* sp., floral buds (1); floral buds - 19. *Coussapoa asperifolia*, pistillate inflorescences (1); inflor. - 20. *Dialium guianense*, aril (1); part of infruct. - 21. *Dioscorea trifida* (?), y. leaves (1); no drawing - 22. *Ephedranthus guianensis*, mesocarp (1); a. infruct. b. seed - 23. *Euterpe oleracea*, whole fruit (1); part of infruct. - 24. *Hymenolobium petraeum*, y. leaves (1); leaflet - 25. *Leretia cordata*, whole fruit (1); a. fruit b+c. stone, lateral views - 26. *Licania micrantha*, bark (1) - 27. *Parkia nitida*, inflor., esp. the stamens and styles of the fertile flowers at the top (1); a. inflor. b. sterile flowers c. fertile flowers d. leaflet 28. *Passiflora glandulosa*, whole fruit (1); a. fruit b. longitudinal section, showing the seeds - 29. *Paullinia tricornis*, aril (1); a+b. two types of fruit - 30. *Philodendron scandens*, infruct. (1); part of infruct. - 31. *Strychnos tomentosa*, mesocarp (1); a. fruit b+c. seed, lateral views - 32. *Virola melinonii*, y. leaves (1) - 33. *Honey* (1)

In total: 33 food items
29 food plant species 71 feeding records
1 honey

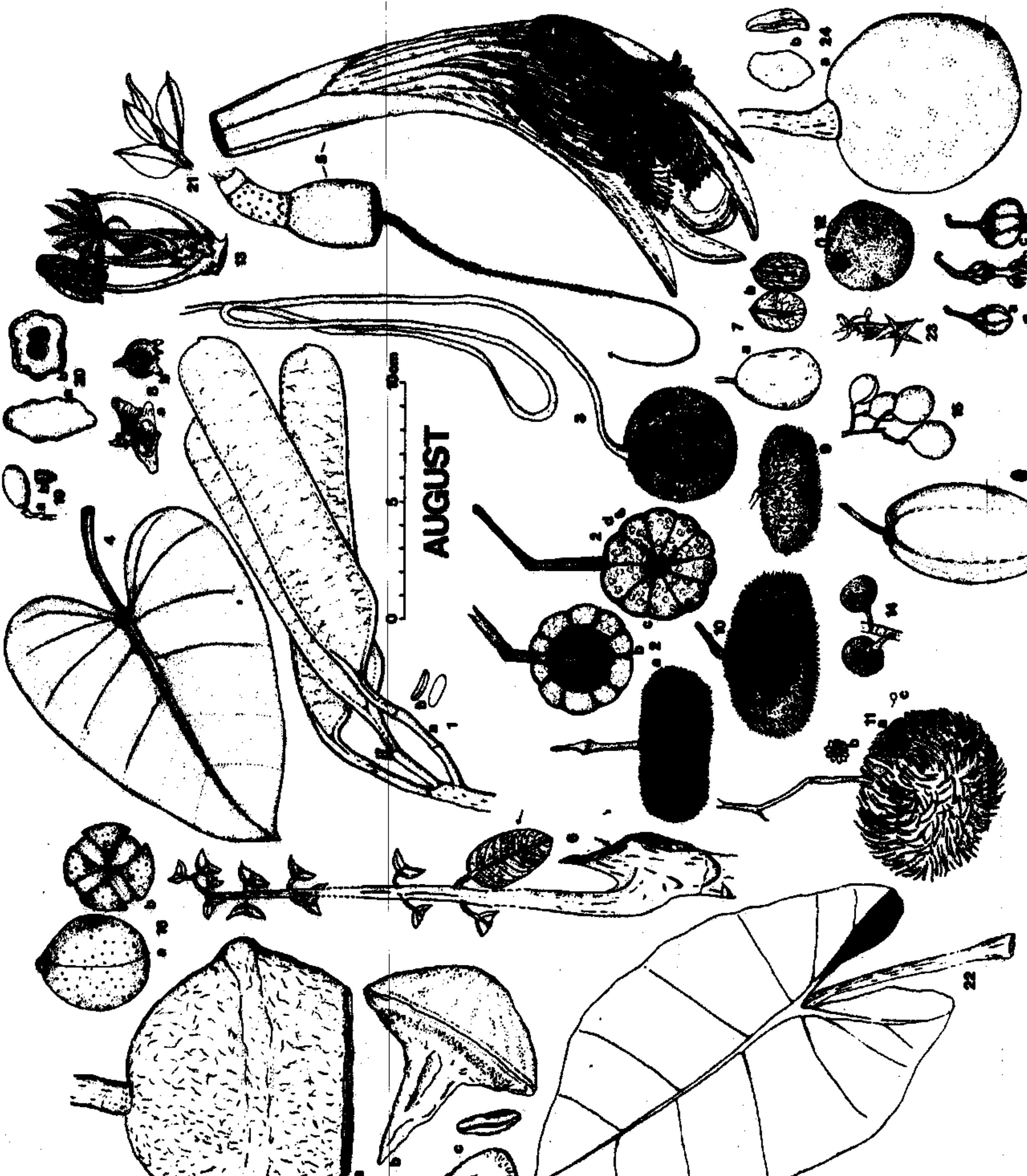

AUGUST
0
5
10cm
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26

Figure 19. Diet in August

1. *Dimorphandra multiflora*, desiccated mesocarp (6); a. part of infruct. b. seed, lateral views - 2. *Apeiba echinata*, mesocarp (5); a. fruit b. fruit from below, the exocarp removed c. fruit from above, the exocarp removed d. seed - 3. *Parkia pendula*, inflor., esp. the tips of flowers (5); inflor., part of the flowers eaten by the monkey - 4. *Philodendron scandens*, y. leaves (4) - 5. *Bombax spectabile*, flowers (2) - 6. *Carapa procera*, y. leaves (2) - 7. *Leretia cordata*, whole fruit (2); a. fruit b. stone, lateral views - 8. *Paullinia tricornis*, aril (2); a+b. two types of fruit - 9. *Apeiba glabra*, mesocarp (1); fruit - 10. *Apeiba schomburgkii*, mesocarp (1); fruit - 11. *Apeiba tibourbou*, mesocarp (1); a. fruit b. several seedlets with mesocarp c. seedlet - 12. *Bagassa guianensis*, y. infruct. (1) - 13. *Bombax spectabile*, y. leaves (1); shoot with young leaves - 14. *Coussapoa angustifolia*, infruct. (1) - 15. *Dialium guianense*, aril (1); part of infruct. - 16. *Guarea kunthiana*, aril (1); a. fruit b. dehiscing fruit from above - 17. *Jacaratia spinosa*, whole fruit (1); a. fruit b. seed - $^{+}$18. *Lecythis davisii*, mesocarp (1); opened fruit b. operculum c. seed, lateral views - 19. *Minquartia guianensis*, whole fruit (1); a. fruit b. stone - 20. *Parinari excelsa*, exocarp + mesocarp (1); a. fruit b. cross section - 21. *Peperomia glabella*, y. leaves (1) - 22. *Philodendron acutatum*, y. leaves (1) - 23. *Sterculia excelsa*, flowers (1); part of inflor. - 24. *Strychnos tomentosa*, mesocarp (1); a. fruit b. seed, lateral views - 25. *Symphonia globulifera*, flowers (1); a. floral bud b. flower, the petals removed c. flower d. stigma from above

In total: 25 food items 45 feeding records
24 food plant species

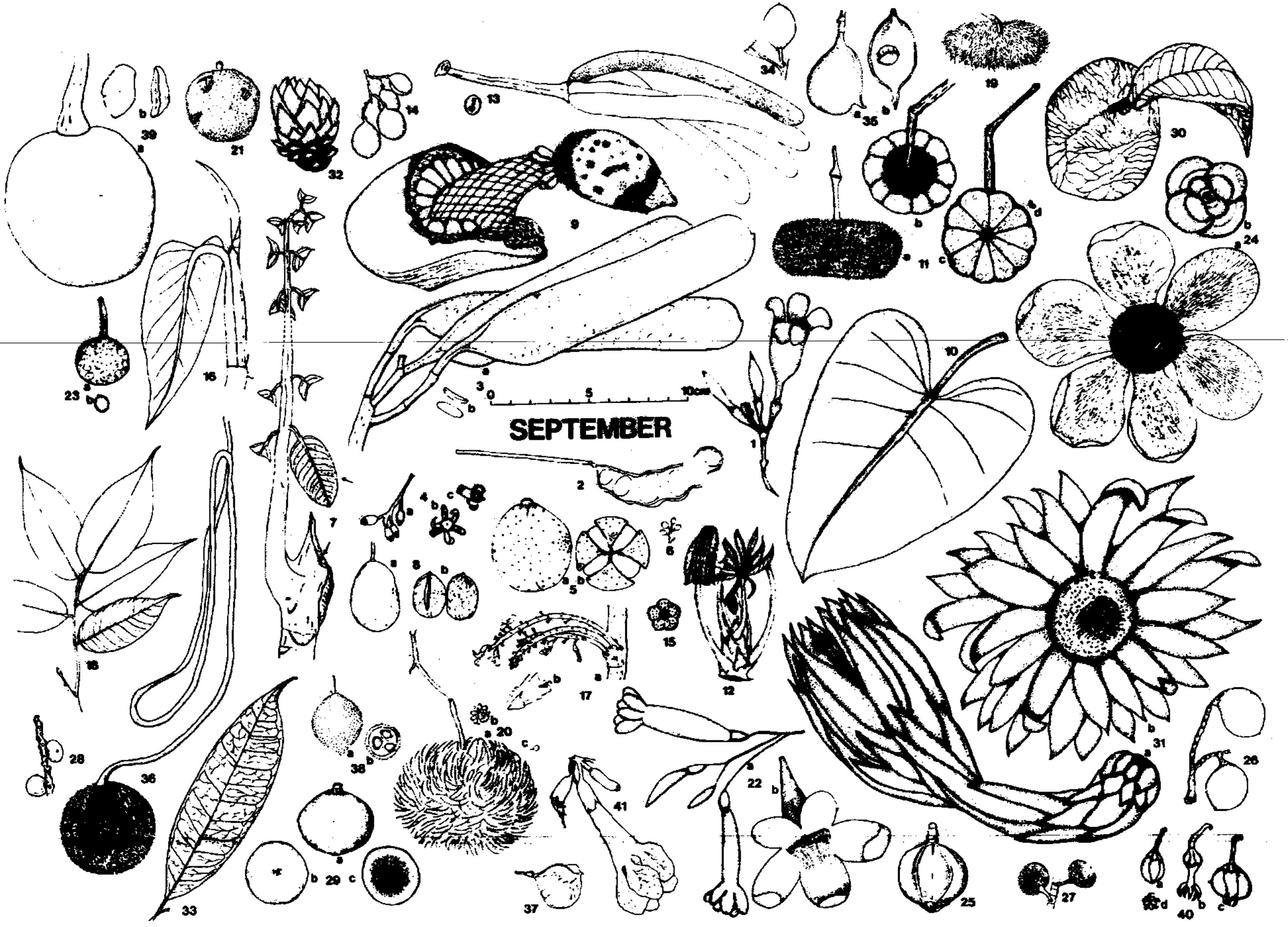

SEPTEMBER
0
5
10cm
1
2
3
a
b
4
a
b
c
5
a
b
6
7
8
a
b
9
10
11
a
b
c
d
12
13
14
15
16
17
a
b
18
19
20
a
b
c
21
22
a
b
23
a
b
24
a
b
25
26
27
28
29
a
b
c
30
31
a
b
32
33
34
35
a
b
36
37
38
a
b
39
a
b
40
a
b
c
d
41

Figure 20. Diet in September

1. *Adenocalymna* sp., flowers (11); part of inflor. - 2. *Inga leiocalycina*, mesocarp (9) - 3. *Dimorphandra multiflora*, desiccated mesocarp (7); a. part of infruct. b. seed, lateral views - 4. *Guarea grandifolia*, flowers (7); a. part of inflor. with floral buds b. flower from above c. flower, lateral view - 5. *Guarea kunthiana*, aril (6); a. fruit b. dehiscing fruit from above - 6. *Hyeronima laxiflora*, whole fruit (5); part of infruct. - 7. *Carapa procera*, y. leaves + base of petiole (3) - 8. *Leretia cordata*, whole fruit (3); a. fruit b. stone, lateral views - 9. *Philodendron acutatum*, infruct. (3); infruct., most of the fruits eaten by the monkey - 10. *Philodendron scandens*, y. leaves (3) - 11. *Apeiba echinata*, mesocarp (2); a. fruit b. fruit from below, the exocarp removed c. fruit from above, the exocarp removed d. seed - 12. *Bombax spectabile*, y. leaves (2); shoot with y. leaves - 13. *Cecropia sciadophylla*, infruct. (2) - 14. *Dialium guianense*, aril (2); part of infruct. - 15. *Guazuma ulmifolia*, whole fruit or mesocarp (2); fruit from above - 16. *Philodendron* sp., tips of shoots + y. leaves (2); shoot with y. leaves - 17. *Platymiscium ulei*, flowers (2); a. inflor. b. flower - 18. *Pterocarpus officinalis*, y. leaves (2); y. leaf - 19. *Apeiba glabra*, mesocarp (1); fruit - 20. *Apeiba tibourbou*, mesocarp (1); a. fruit b. several seeds with some mesocarp c. seed - 21. *Bagassa guianensis*, y. infruct. (1) - 22. *Arrabidaea corallina*, flowers (1); a. part of y. inflor. b. opened corolla, obliquely from above - 23. *Brosimum parinarioides*, infruct. (= pseudofruit) (1); a. infruct. b. seed - 24. *Clusia platystigma*, male flowers, esp. central body of staminodes (1); a. flower from above, showing the central body of staminodes b. flower from below, the petals removed, showing bracteola and sepals - 25. *Clusia purpurea*, pulp (= many seedlets with aril) (1); fruit - 26. *Copaifera epunctata*, aril (1); infruct. - 27. *Coussapoa angustifolia*, infruct. (1) - 28. *Euterpe oleracea*, whole fruit (1); part of infruct. - 29. *Ficus insipida*, whole fig (1); a. fig b. fig from above c. cross section - 30. *Helicostylis pedunculata*, infruct. (1); infruct., one leaf attached - 31. *Hylocereus* sp. a., flowers, esp. tips of stamens and style, and stigma (1); a. flower b. flower from above - 32. *Hylocereus* sp. b., flowers, esp. the tips (1); flower, the tip eaten by the monkey - 33. *Maquira guianensis*, y. leaves (1) - +34. *Micropholis guyanensis*, mesocarp - 35. *Ormosia paraensis*, y. seeds (1); a. fruit b. fruit, one valve removed, showing the mimetic seed - 36. *Parkia pendula*, inflor., esp. the tips of flowers (1); inflor. with part of peduncle, part of the flowers eaten by the monkey - 37. *Peltogyne venosa*, aril (1); fruit - 38. *Rheedia benthamiana*, aril (1); a. fruit b. cross section showing the seeds - 39. *Strychnos tomentosa*, mesocarp (1); a. fruit b. seed, lateral views - 40. *Symphonia globulifera*, flowers (1); a. floral bud b. flower, the petals removed c. flower d. stigma from above - 41. *Tabebuia serratifolia*, flowers (1); part of inflor., the corolla of one flower eaten by the monkey

In total: 41 food items 96 feeding records
41 food plant species


OCTOBER
0
5
10cm
1
2
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48

Figure 21. Diet in October

1. *Ecclinusa guianensis*, mesocarp (71); a. fruit b. cross section, showing the seeds c. seed - 2. *Dimorphandra multiflora*, desiccated mesocarp (24); a. part of infruct. b. seed, lateral views - 3. *Achrouteria pomifera*, mesocarp (17); a. fruit b. fruit from below c. seed, lateral views d. cross section, showing the seeds - 4. *Guarea grandifolia*, flowers (11); a. part of inflor. with floral buds b. flower from above c. flower, lateral view - 5. *Philodendron scandens*, y. leaves (10) - 6. *Arrabidaea courallina*, flowers (9); a. part of y. inflor. b. opened corolla, obliquely from above - 7. *Abuta grandifolia*, mesocarp (7); a. part of infruct. with two types of fruit b. stone - 8. *Hylocereus* sp. a., flowers, esp. tips of stamens and style, and stigma (5) - 9. *Pterocarpus officinalis*, y. leaves (5); y. leaf - 10. *Bagassa guianensis*, y. infruct. (4) - 11. *Helicostylis pedunculata*, infruct. (4); infruct., one leaf attached - 12. *Vataireopsis speciosa*, y. leaves (4) - 13. *Carapa procera*, y. leaves + base of petiole (3) - 14. *Adenocalymna* sp., flowers (2) - 15. *Dystictis* vs. *granulosa*, y. leaves (2); no drawing - 16. *Bombax spectabile*, y. leaves (2); shoot with y. leaves - 17. *Dipteryx odorata*, y. leaves (2); y. leaf - 18. *Ephedranthus guianensis*, mesocarp (2); a. infruct. b. seed - 19. *Hylocereus* sp. b., flower, esp. the tip (2); flower, the tip eaten by the monkey - 20. *Parkia nitida*, mesocarp (2); infruct., few fruits left - 21. *Strychnos tomentosa*, mesocarp (2); a. fruit b. seed, lateral views - 22. *Virola melinonii*, aril (2); a. dehiscing fruit b. fruit, one valve removed, showing the seed with lacerate aril c. seed - 23. *Ampelocera edentula*, y. leaves (1); y. leaf - 24. *Apeiba echinata*, flowers (1); a. floral bud b. flower c. flower, the sepals and petals removed - 25. *Apeiba glabra*, mesocarp (1); fruit - 26. *Bellucia grossularioides*, whole fruit (1); a. fruit b. fruit from above - 27. *Dystictis* vs. *granulosa*, flowers, esp. the corolla (1) - 28. *Brosimum lactescens*, infruct. (= pseudofruit) (1); a. two-seeded infruct. b. three-seeded infruct. c. seed - 29. *Carapa procera*, flowers (1); a. flower b. flower from above - 30. *Clarisia racemosa*, whole fruit (1); a+b. two types of fruit c. seed - 31. *Cupania* sp., whole fruit (1); infruct. - 32. *Cupania* sp., y. leaves (1); no drawing - 33. *Fagara* sp., y. leaves (1); y. leaf - 34. *Ficus nymphaeifolia*, whole fig (1); a. figs and leaves, strongly reduced b. fig - 35. *Goupia glabra*, whole fruit (1); infruct. - 36. *Guarea grandifolia*, aril (1); a. fruit b. dehiscing fruit from above c. stone without aril, lateral views d. stone with aril, lateral views - 37. *Guatteria chrysopetala*, whole fruit (1); infruct. - 38. *Gustavia hexapetala*, mesocarp + funicle (1); a. fruit from below b. seed, lateral views - 39. *Not identified species* (Loranthaceae), y. leaves (1) - 40. *Moutabea guianensis*, mesocarp (1); a. fruit b. fruit from below c. cross section, showing the seeds - 41. *Parinari excelsa*, exocarp + mesocarp (1); a. fruit b. cross section - 42. *Philodendron acutatum*, y. leaves (1) - 43. *Quassia simarouba*, bark (1) - 44. *Tabebuia serratifolia*, flowers (1); part of inflor., the corolla of one flower eaten by the monkey - 45. *Tabebuia serratifolia*, y. leaves (1); y. leaf - 46. *Unonopsis glaucopetala*, whole fruit (1); a. fruit b. seed, lateral views - 47. *Vitex stahelii*, whole fruit or mesocarp only (1); a. fruit b. fruit from above c. fruit from below d. stone - 48. *Caterpillars*, whole insects (1)

In total: 48 food items
43 food plant species 222 feeding records
1 insect species


NOVEMBER
0 5 10cm
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15-35-47
55-56
57-60
65
67
16
17
18
19
20
21
22
23
24
25
26
27
28
30
31
32
33
34
36
37
38
39
40
41
42
43
44
45
46
48
49
50
51
52
53
54
58
59
61
62
63
64
66
68
69
70

Figure 22. Diet in November

1. Achrouteria pomifera, mesocarp (31); a. fruit b. fruit from below c. cross section, showing the seeds d. seed, lateral views - 2. Guatteria chrysopetala, whole fruit (18); infruct. - 3. Brosimum lactescens, infruct. (11); a. two-seeded infruct. b. three-seeded infruct. c. seed - 4. Coussapoa latifolia, infruct. (11); a. twig with infruct., strongly reduced b. infruct. - 5. Ceiba pentandra, y. leaves (10); y. leaf, esp. the apical part of the leaflets eaten - 6. Philodendron acutatum, infruct. (10); part of infruct., most of the fruits eaten by the monkey - 7. Bagassa guianensis, infruct. (9) - 8. Vataireopsis speciosa, y. leaves (9) - 9. Ficus gardneriana, whole fig (8); a. fig b. fig from above - 10. Ampelocera edentula, flowers (7); part of inflor. - 11. Dimorphandra multiflora, desiccated mesocarp (7); a. part of infruct. b. seed, lateral views - 12. Guarea grandifolia, aril (7); a. fruit b. dehiscing fruit from above c. stone without aril, lateral views d. stone with aril, lateral views - 13. Bellucia grossularioides, whole fruit (6); a. fruit b. fruit from above - 14. Brosimum parinarioides, infruct. (6); a. y. infruct. b. mature infruct. c. seed - 15. Licania micrantha, bark (6) - 16. Cordia sagotii, whole fruit (5); a. fruit b. fruit from below c. stone - 17. Ecclinusa guianensis, mesocarp (5); a. fruit b. cross section, showing the seeds c. seed - 18. Carapa procera, flowers (4); a. flower b. flower from above - ++19. Couepia caryophylloides, exocarp + mesocarp (4); a. fruit b. stone - 20. Peperomia glabella, y. leaves (4)- 21. Unonopsis glaucopetala, whole fruit (4); a. infruct. b. seed, lateral views - 22. Virola melinonii, aril (4); a. just dehiscing fruit b. fruit, one valve removed c. seed with aril - 23. Cecropia sciadophylla, infruct. (3) - 24. Ceiba pentandra, floral buds + flowers (3); inflor. - 25. Clarisia racemosa , whole fruit (3); a+b. two types of fruit c. seed 26. Gnetum urens, perigonium or whole fruit (3); a. infruct. b. seed - 27. Apeiba echinata, flowers (2); a. floral bud b. flower c. flower, the sepals and petals removed - 28. Bagassa guianensis, y. infruct. (2) - 29. Dystictis vs. granulosa, y. leaves (2); no drawing - 30. Dystictis vs. granulosa, y. seeds (2); a. fruit b. suture c. fruit, one valve removed, showing the seeds d. seed - 31. Carapa procera, y. leaves + base of petiole (2); leaf - 32. Ceiba pentandra, exocarp of y. fruits (2); a. y. fruit b. seed - 33. Ficus broadwayi, whole fig (2); a. fig b. fig from above c. cross section - 34. Gustavia hexapetala, mesocarp + funicle (2); a. fruit from below b. seed, lateral views - 35. Inga alba, bark (2) - 36. Pereskia aculeata, flowers (2) - 37. Pterocarpus officinalis, y. leaves (2); leaf - 38. Talisia sylvatica, mesocarp (2); a. infruct., one fruit eaten out by the monkey b. seed - 39. Trichilia surinamensis, whole fruit (2); a. fruit b. fruit, two valves removed c. seed - 40. Abuta grandifolia, mesocarp (1); a. part of infruct. with two types of fruit b. stone - 41. Ampelocera edentula, y. leaves (1) - 42. Apeiba glabra, mesocarp (1); fruit - 43. Attalea speciosa, decaying and rotten sheaths (1) - 44. Xylophragma seemannianum, flowers (1) - 45. Cedrela odorata, y. seeds + columella (1); a. y. fruit b. mature fruit c. seed - 46. Coussapoa angustifolia, infruct. (1) - 47. Dimorphandra multiflora, bark (1) - 48. Stizophyllum inaequilaterum, flowers (1) - 49. Eperua falcata, flowers (1) - 50. Euterpe precatoria, whole fruit (1); a. fruit from below b. stone - 51. Fagara sp., y. leaves (1); leaf - 52. Ficus malacocarpa, whole fig (1); a. infruct. b. fig from above - 53. Ficus trigona, whole fig (1); a. twig with infruct., strongly reduced b. infruct. c. fig from above - 54. Guarea grandifolia, flowers (1); a. part of inflor. b. flower from above c. flower, lateral view - 55. Hyeronima laxiflora, bark (1) - 56. Inga leiocalycina, bark (1) - 57. Licania majuscula, bark (1) - 58. Licania micrantha, y. leaves (1) - 59. Licaria canella, y. leaves (1) - 60. Nectandra cf. kunthiana, bark (1) - 61. Norantea guianensis, flowers, esp. the honeycups (1); part of


DECEMBER
10cm
5
0
1
2 a b c
3
4 a b c d
5
6 a b c d
7 a b c
8
9 a b
10
11
12 a b
13
14 a b
15 a b
16
17 a b
18 a b c
19
20
21
22
23-27
24 a b
25 a b c
28
29 a b c
30
31
32
33 a b c d
34
35 a b
36-37
38 a b
39
40
41
42
43
43 a b
44
45
46
47 a b

Figure 22 (continued)

inflor. - 62. Operculina alata, y. seeds (1); a. floral bud b. flower from above c. seed - 63. Parkia nitida, mesocarp (1); infruct., two fruits left - 64. Philodendron scandens, y. leaves (1) - 65. Pithecellobium jupunba, bark (1) - 66. Qualea dinizii, flowers (1); flower - 67. Sacoglottis cydonioides, bark (1) - 68. Tabebuia capitata, flowers (1); part of inflor. - 69. Trymatococcus oligandrus, whole fruit (1); a. fruit b. fruit from above - 70. Vitex stahelii, whole fruit or mesocarp only (1); a. fruit b. fruit from above c. fruit from below d. stone

In total: 70 food items 255 feeding records
45 food plant species

Figure 23. Diet in December

1. Bagassa guianensis, infruct. (20) - 2. Clarisia racemosa, whole fruit (14); a+b. two types of fruit c. seed - 3. Guatteria chrysopetala, whole fruit (13); infruct. - 4. Achrouteria pomifera, mesocarp (11); a. fruit b. fruit from below c. cross section, showing the seeds d. seed, lateral views - 5. Vataireopsis speciosa, y. leaves (9) - 6. Vitex stahelii, whole fruit or mesocarp only (8); a. fruit b. fruit from above c. fruit from below d. stone - 7. Brosimum parinarioides, infruct. (7); a. y. infruct. b. mature infruct. c. seed - 8. Inga alba, mesocarp (6); fruit - 9. Bellucia grossularioides, whole fruit (5); a. fruit b. fruit from above - 10. Xylophragma seemannianum, flowers (4); part of inflor. - 11. Ceiba pentandra, y. leaves, esp. the apical part of the leaflets (4); leaf - 12. Dimorphandra multiflora, desiccated mesocarp (4); a. part of infruct. b. seed, lateral views - 13. Cecropia sciadophylla, infruct. (3) - 14. Ceiba pentandra, exocarp of y. fruits (3); a. y. fruit b. seed 15. Trichilia surinamensis, whole fruit (3); a. part of infruct. b. dehiscing fruit from above - 16. Ampelocera edentula, y. leaves (2) - 17. Cedrela odorata, y. seeds + columella (2); a. y. fruit b. mature fruit c. seed - 18. Cordia sagotii, whole fruit (2); a. fruit b. fruit from below c. stone - 19. Coussapoa latifolia, infruct. (2); a. twig with infruct., strongly reduced b. infruct. - 20. Philodendron acutatum, aerial roots, esp. the tips (2); part of aerial root - 21. Philodendron acutatum, infruct. (2); infruct., part of the fruits eaten by the monkey 22. Philodendron acutatum, y. leaves (2) - 23. Sacoglottis cydonioides, bark (2) - 24. Unonopsis glaucopetala, whole fruit (2); a. infruct. b. seed, lateral views - 25. Apeiba echinata, flowers (1); a. floral bud b. flower c. flower, the sepals and petals removed - 26. Dystictis vs. granulosa, y. leaves (1); no drawing - 27. Couratari stellata, bark (1) - 28. Coussapoa asperifolia, infruct. (1) - 29. Eschweilera congestiflora, y. seeds + aril (1); a. fruit b. fruit, the operculum removed c. seed - 30. Ficus americana, whole fig (1); twig with infruct. - 31. Ficus citrifolia, whole fig (1); infruct. - 32. Not identified species (Gesneriaceae), y. leaves (1) - 33. Guarea grandifolia, aril (1); a. fruit b. dehiscing fruit from above, showing the stones c. stone without aril, lateral views d. stone with aril, lateral views - 34. Hillia illustris, flowers, esp. the corolla (1); corolla - 35. Hylocereus sp. a., flowers, esp. the tips of stamens and style, and stigma (1); a. flower from above b. flower just before opening - 36. Inga alba, bark (1) - 37. Inga leiocalycina, bark (1) - 38. Leretia sp., exocarp + mesocarp (1); a. fruit b. stone - 39. Licania majuscula, exocarp + mesocarp (1); fruit, the exocarp and mesocarp partly scraped off by the monkey - 40. Licaria canella, y. leaves (1) - 41. Maquira guianensis, y. leaves (1) - 42. Species b. (Orchidaceae), pseudobulbs (1) - 43. Paullinia sphaerocarpa, y. seeds (1); a. infruct. b. valve from inside - 44. Peperomia glabella, y. leaves (1) - 45. Pereskia aculeata, flowers (1) - 46. Philodendron scandens,

Figure 23 (continued)

y. leaves (1) - 47. Pouteria sp., y. seeds (1); a. y. fruit b. cross section c. y. seed - 48. Tabebuia serratifolia, y. leaves (1); y. leaf

In total: 48 food items 155 feeding records
45 food plant species

4.3. Ateles as Specialized Frugivore

Among frugivores, two major categories are distinguishable in between, of course, a continuum exists:

1. 'Total frugivores' (Morton, 1973) or 'specialized frugivores' (McKey, 1975)
2. 'Partial frugivores' (Morton, 1973) or 'opportunistic frugivores' (McKey, 1975).

Specialized frugivores derive most of their supplies of carbohydrate, lipid and protein from fruits. They are restricted to the tropics. For instance, several cotingids (e.g., the bellbird), the oilbird, several trogons (e.g., the quetzal), most toucans, several bats and the spider monkey are specialized frugivores.

Opportunistic exploiters of fruits utilize fruits primarily as a source of carbohydrates and water. Representatives of this category may be primarily insectivorous, even as adults, or they may subsist mostly on fruits as adults, feeding their young with insects. In general, these animals exploit fruits as a quickly harvestable supply of carbohydrates, water and possibly minerals and vitamins not interfering much with the harvest of proteins and lipids from other sources (e.g., insects, meat). The majority of Neotropical birds and monkeys belong to the second category. For instance, trumpeters, curassows, guans, chachalacas, quails, tinamous, woodpeckers, caciques, tanagers, oropendulas, manakins, trushes, wood warblers, tyrant flycatchers, squirrel monkeys, capuchin monkeys and callitrichid monkeys are opportunistic fruit eaters.

In general, fruits eaten by specialized frugivores are characterized by a firm, dense edible part (aril or mesocarp), rich in fats and proteins, and by one or few large seeds, whereas fruits ingested by a wide variety of animals have juicy, watery flesh and contain (usually many) small seeds (e.g., Ficus, Miconia, Cecropia). Large-seeded nutritious fruits seem to have coevolved with specialized frugivores as their principal dispersal agents (B.K. Snow, 1970; D.W. Snow, 1971; Snow and Snow, 1971).

Two coevolutionary patterns can be distinguished between fruits and dispersal agents: the higher quality of dispersal performed by a relatively small subset of specialized frugivores, and the greater quantity of dispersal delivered by a wide array of opportunistic animals.

As McKey (1975) pointed out, the evolution of adaptations to specialized frugivory has resulted in generally increased dispersal quality. Specialized frugivores are more dependent on fruits as food, and one may expect that they possess a better ecological knowledge of available food sources (like spider monkeys with their well-developed spatial and temporal memory). Their reliability of visitation to the fruit-crops they exploit means that the chance is minimized that mature fruits remain on the plant and become rotten or desiccated, or predated on the forest floor. Furthermore, the quality of dispersal depends on the treatment of the seeds inside the gut of the dispersal agent. Seeds adapted to dispersal by ingestion (endozoochory) possess protection from the rough chemistry and/or physics experienced inside the guts of animals. This defence can be a hard seed coat or endocarp. Many specialized frugivores do have little-muscularized, thin-walled, often small stomachs,

reflecting a relatively small amount of mechanical breakdown necessary for digestion of fruit flesh (Jenkins, 1969).
Another feature of many specialized frugivores, in particular birds, is the habit of regurgitating larger seeds just after the surrounding edible part has been removed in the stomach. For the plant both these features mean that seeds ingested by specialized frugivores would receive a gentle treatment within the gut. Spider monkeys can not regurgitate seeds, but they do not masticate much and seldom destroy seeds with the teeth.
Coevolution with specialized frugivores should involve the possibility of evolving relatively soft seeds, not protected by a tough layer of endocarp. This pattern of coevolution may be seen in Lauraceae, producing nutritious fruits containing one large, vulnerable seed, protected from exploitation by non-specialized animals thanks to its size and toxic compounds in it. This family figures strongly in the diets of a number of specialized fruit-eaters (Snow, 1971).
Large seeds have a greater store of reserves than small seeds, so that, in general, a habitat contains a greater number of safe sites for larger seeds than for small seeds. In some environments, selection favours an increase in seed size and a corresponding decrease in seed number (Janzen, 1969). The plant is permitted to evolve larger seeds (if this would increase its fitness), provided it produces a fruit nutritious enough to attract specialized frugivores capable of ingesting large seeds in terms of energy expended on transporting and expelling the ballast. The high nutritive content of these large-seeded fruits is notable. This coevolutionary pattern may be demonstrated in families as Palmae, Burseraceae, Myristicaceae, Sapindaceae, Loganiaceae, Capparaceae, Sapotaceae and Meliaceae, all producing important edible fruits for spider monkeys.

Why invests a plant so much energy per propagule in the production of fat and protein-rich fruits, in a physical environment so poor on minerals and other anorganic compounds, as, in general, can be said for tropical rain forest?
According to McKey (1975), the production of nutritious fruits has to be viewed as the principal cost of high-quality dispersal. Many animals feed primarily on insects and only utilize fruits as a source of water and carbohydrates (Morton, 1973). Plants depending on such animals for their seed dispersal may be able to attract them with relatively inexpensive, low-nutritious fruits (often berries). Opportunistic animals will choose to ingest a berry with small seeds rather than a protein-rich fruit with a large seed, as long as proteins and lipids can be derived more easily from other sources (like from insects). On the other hand, an animal that is dependent on fruits for all its dietary requirements will select the most nutritious fruits of the available array, and adapt to the annoyances such as large seeds, which may accompany these nutritious fruits. Obviously, this is true for spider monkeys. About 80% of the 166 plant species producing edible fruits, used by Ateles p. paniscus, is nutritious and large-seeded. Juicy, relatively low-nutritious and small-seeded fruits like of Hylocereus, Pereskia, Jacaratia, Bellucia, Coussapoa, Ficus, Trymatococcus, Campomanesia, Guettarda and Passiflora make up only 20% of the total number of fruit species eaten. Moreover, all these fruits were usually exploited incidentally by the spider monkeys on the way from one nutritious fruit source to another, and appeared never to significantly influence the daily foraging route. Also, regularly revisiting food sources of this kind was not performed.

How are opportunistic fruit eaters prevented from exploiting nutritious fruits?
At least four measures can be distinguished:

1) The development of large seeds. Many opportunistic fruit eaters are not able to ingest and expel larger seeds or stones.
2) A strong attachment of the edible part (mesocarp or aril) to the seed coat or the endocarp, making it harder or impossible for many animals to separate both in order to ingest only the edible part (e.g., in *Burseraceae* and *Inga*).
3) A toxic seed coat or endosperm, preventing opportunistic fruit eaters from masticating both seeds and pulp before ingesting (e.g., in several *Lauraceae*, *Myristicaceae* and in *Strychnos*).
4) An indehiscent, tough outer layer combined with large seeds and nutritious pulp, possibly an adaptation to dispersal by specialized frugivorous monkeys (e.g., in *Capparis*, *Parahancornia*, *Strychnos tomentosa* and *Salacia*).

In general, fruits most often eaten by opportunistic animals are characterized by a juicy flesh, containing much water, carbohydrates and organic acids, and small, often many seedlets. When the fruit is small, the outer layer is thin and leathery, whereas in larger fruits the outer layer is easily penetrable or dehiscent. These features can be seen in many *Melastomataceae*, *Myrtaceae*, *Moraceae* (*Ficus*, *Cecropia*), *Guttiferae* (*Clusia*), *Caricaceae* (*Carica*, *Jacaratia*) and *Passifloraceae*.

Compared with carbohydrates, fats yield more than twice as much energy per gram upon catabolism. Carbohydrates, however, give a quicker source of energy. The smaller the animal and the higher the metabolic rate, the more need it has for quick energy in the form of carbohydrates. This may be an additional reason why small fruits with small seeds are usually succulent and contain much carbohydrate rather than fat. In this view, it is interesting that most specialized frugivores are rather large and capable to ingest large seeds.

In the community context, the adaptations of a plant to dispersal in competition with other plants for the service of a limited supply of dispersal agents, can be the following:
1) The evolution of a fruit that is exploitable by a greater variety of dispersal agents. For this purpose, for instance the size of the seeds has to be decreased, but this may come at the cost of decreased dispersal quality.
2) The evolution of a fruit that attracts a specialized group of animals, shared with relatively few other plants as dispersal agents. The rise in dispersal quality entails the cost of producing more nutritious fruits.
3) The evolution of structures for dispersal by inanimate agents (wind, water, the plant itself). The structures involved are probably very inexpensive and a huge number of seeds can be dispersed in a very short period of time, but the disadvantages are that most seeds are not dispersed far from the parent plant, and in particular wind-dispersal is only effective for relatively small seeds. Furthermore, the range of habitats is more restricted.
4) Displacement of fruiting seasons of sympatric species of one genus. Since each species with a broad-niched fruit utilizes a large proportion of the available dispersal agents, when it is fruiting, there should be strong selection for fruiting seasons of such species to be displaced one from another (e.g., *Ficus*).
5) Spreading of the fruit production over a long period of time, so that, at any moment, less strenuous demands are being made on the small community of dispersal agents. Since a plant following this tactic can present only relatively few mature fruits at one time, and the fact that spreading of the fruiting season results in extensive overlap with the fruiting seasons of other plants, demands that plants following this strategy have their own reliable subset of dispersal agents, shared with relatively few other plants.

Since a specialized frugivore must extract a balanced diet from the fruits available to it at any one time, its existence may require overlapping fruiting seasons. This pattern may be shown in the spider monkey. Most nutritious fruit species eaten by *Ateles p. paniscus* have a definite fruiting season. Many of these fruiting seasons are quite long and overlap broadly. Most *Burseraceae*, for instance, fructify during 2 - 3½ months. Other examples are: *Capparis maroniensis* (4½ months), *Dimorphandra multiflora* (7), many *Inga* spp (2 - 3), *Strychnos tomentosa* (7½), *Guarea grandifolia* (4), *Moutabea guianensis* (4), *Euterpe* spp. (2), *Oenocarpus bacaba* (2), *Apeiba* spp. (2 - 3), *Virola melinonii* (5½) and *Licania majuscula* (5).

In most nutritious fruits exploited by spider monkeys, the length of the fruiting season is determined by the individual plants of one species not fruiting simultaneously and by the spread fruit maturing within one plant. For 62 species producing nutritious fruits, the fruiting seasons were determined precisely, of which 52 were fruiting during periods ranging from 2 to 8 months. In contrast, 14 of the 20 low-nutritious fruit species were fruiting during periods of less than 2 months.

Ateles, as a dispersal agent, shows many features of coevolution with nutritious, large-seeded fruits. The high-quality dispersal offered by spider monkeys, among few other specialized frugivores, compensates the cost of producing crops of nutritious fruits for the plant, but severely limits in the number of propagules. The fruiting seasons of these fruits, in general, are often long since the small number of dispersal agents may be easily overloaded by a mass-ripened fruit crop, and the existence of the dispersal agent may require that several species of fruits, each providing different nutrients, have broadly overlapping fruiting seasons.

4.4. Edibility of Spider Monkey Foods for Man

In Surinam, when asked, native Bushnegroes and Amerindians will tell that man can consume most of the fruits that spider monkeys eat, in contrast with howler monkey food. This is true. At least once, every fruit kind belonging to the spider monkey diet was consumed by myself. Most arils and mesocarps were sweet and juicy, some mealy but good to eat. Only in case of the infructescences of *Araceae* (e.g., *Monstera* and *Philodendron* spp.), my blind faith in spider monkey taste was regretted. Its fruits gave a caustic effect in one's mouth, lasting for hours, probably caused by calciumoxalat cristals. By not masticating the fruits, spider monkeys seem to avoid this problem.

Most fruits eaten by spider monkeys are hardly worthwhile to spend time and energy on for food. The edible part of most fruits is small or even tiny and the only way to get some digestable quantity in one's stomach is to swallow lots of whole fruits or drop only the outer layer like spider monkeys usually do.

In general, the fruits of almost all *Burseraceae*, *Sapotaceae*, *Moraceae*, *Annonaceae*, *Boraginaceae*, *Cactaceae*, *Passifloraceae*, *Guttiferae* and *Inga* are good to eat. Even the young seeds and flush leaves, eaten by spider monkeys, were consumed by me without special regrets.

5. FEEDING BEHAVIOUR

5.1. A Spider Monkey Day

To introduce the main text, an outline of the spider monkey daily activities will be presented with special emphasis on feeding behaviour.
A day typical for the long wet season will be compared with one typical

for the long dry season, since feeding behaviour appeared to be influenced strikingly by the seasons.

5.1.1. A spider monkey day during the long wet season. In Surinam, day dawns at 5.45 h local time. At first light, when it is still almost dark beneath at the forest floor, a subgroup of spider monkeys, forming part of a group or community, moves out of the huge, isolated crown of a 50 m tall Hymenolobium flavum, its sleeping tree for the passed night at the foot of the Voltzberg. Just before leaving, the area beneath its crown is bombed by enormous amounts of excreta as the members of the subgroup urinate and defecate almost simultaneously. The old female with her son, a juvenile-3, is the first to move. The others, a female with her daughter, a juvenile-2, and an old male follow in a row. Soon, they reach a group of food trees not far from the sleeping tree, apparently one of the reasons for choosing this particular tree last night. After feeding on four trees from 6.00 - 7.00 h, without once feeding all together on the same tree, they travel over one kilometer within 20 minutes. All the way, the old female determines the route and the activity patterns of the subgroup as a whole. At once, the female with the juvenile-2 splits off. Apparently, she has a different foraging route in mind, connecting other food sources, than the old female has. Within short time, they are out of sight and we will follow the old female, her son and the old male.
Before 8.00 h, they feed together on another two trees. At 8.00 h, the female starts to bark, immediately followed by the male, resulting in a siamang-like barking duet. It seems to act as a kind of distant call that differs much from the long call only adult males are able to give. It will let others know its location of the moment.
After feeding on another tree, the monkeys rest about half an hour. After another feeding bout of 15 minutes in the same tree, they travel fast over 500 m. After feeding shortly, they start another barking duet in which the juvenile tries to take part. Then, they feed again for 20 minutes on the same tree. Between 10.15 - 12.15 h, the monkeys feed on ten different trees following a route of 500 m, still fully determined by the old female. After that, they rest for 40 minutes in the upper part of the canopy. The old female lies on her back in a fork of branches, closing her eyes.After feeding another 15 minutes in a nearby tree, they rest again about half an hour. At 14.00 h, they travel away and soon join another subgroup. This subgroup usually ranges most of the time in another 'core area' within the home range inhabited by the group. It counts four animals, two females, a male juvenile-2 and a dependent infant 1-2. After a greeting ceremony, usually performed only by the males in such occasions, but this time also by the females embracing one another shortly, the juveniles start to play, whereas the adults rest for 45 minutes in an emergent tree. At the beginning of the resting period, the old male gives a long call, answering another male about 500 m away. At 14.45 h, all seven animals travel and feed for 20 minutes on two nearby trees, whereas the juveniles keep on playing. Then, they travel in about the same direction as 'our' subgroup came from, before joining took place. After travelling and feeding shortly, the other subgroup splits off at 16.00 h, moving very fast in the direction of the long call heard just before produced by the third male of the group. 'Our' subgroup follows them for a short time but soon returns on its way. At this point, they are in the same area as they were this morning at 8.00 h. Apparently, the route planned for today by the old female is disarranged considerably. After feeding on two trees, 'our' subgroup moves back the way they just came, but then turns more to the north. Now, they seem to be in a hurry travelling very fast over 600 m. I have many troubles in tracking them. Another male is calling nearby

and some minutes later we meet a young male who joins the subgroup after a short greeting ceremony between the three males. Immediately after, the two adult males start a barking duet. Then, the newcomer travels away, followed by the other males. The old female, so far leading the subgroup today, stays far back. She enters the lower part of the canopy here or the top of a tall tree there, in search of new food sources. Several fruiting trees are checked by her on the stage of maturity, whereas the males are rushing forwards in the direction of the sleeping tree for the coming night, some 500 m away. Somewhat later, the old male travels in front of the male subgroup whereas the female follows at a distance of about 50 m. After feeding together on one tree, all four travel towards the sleeping tree at 17.15 h, the female in front. Till 18.00 h, they feed on another four trees in the direct neighbourhood of the sleeping tree. Part of the time, the juvenile plays with the young male, playfighting and chasing each other. From 18.00 - 18.30 h, they feed on another three trees next to the large buttressed sleeping tree, a *Newtonia suaveolens*. At 18.30 h, the young male goes away to another sleeping tree. Ten minutes later, the old male and the juvenile enter the sleeping tree by crossing a gap between two crowns, swaying hin and back, grasping the extreme twigs of a crownlet of the sleeping tree and sweeping across. Some minutes later, the female enters the tree in the same way and all three feed for a while on the inflorescences of the sleeping tree itself and on the young leaves of two epiphytes, members of the *Araceae*, hanging down along the huge bole of the tree. At 18.40 h, when it is almost dark on the forest floor, the monkeys prepare for the night, each on its own place. The juvenile rests against his mothers belly for a while, then moves to his own place some 6 m away from her. When I finally reach the camp, it's completely dark on the forest floor.

Today, the three animals observed continuously, had been feeding on a total of 38 different food plants belonging to 13 species, of which two were very important. Of the first, *Virola melinonii*, the monkeys used 17 different trees, of the second, *Laetia procera*, they used 6 different trees. A total of 32 feeding records was made on fruits (not including the data from faeces), 4 on flowers and 2 on young leaves. Total feeding time was 5½ hours, total resting time between 6.00 - 18.45 h was 3 hours, and total travel distance was 4500 m.

5.1.2. **A spider monkey day during the long dry season.** When I reach this night's sleeping tree at 06.00 h, the sky is clear. The spider monkeys are still resting high up in the crown of a 50 m tall *Vochysia tomentosa*. The crown is completely isolated from the canopy beneath and hard to enter. This subgroup contains an old female and her juvenile son of about three years old, the same animals as followed in the first example (among others), and a second adult female. At about 6.30 h, all animals defecate. The faeces are compact, containing mainly vegetable matter and few seeds of only one species. Sitting side by side, the mother leans over her son and nurses him for two minutes. Over three years old, he is still nursed from time to time. Within one or two months he will be weaned, and shortly after his mother will come in estrus for the first time after approx. four years.
At 6.45 h, the second female descends to the canopy by leaping across a gap. Mother and son keep on resting. Twenty minutes later, they also move out of the sleeping tree and join the other female some 120 m away, who was waiting for them, uttering soft contact calls. Together, they travel about 100 m towards a fruiting tree of the most important food species of the moment, *Dimorphandra multiflora*, offering edible pods for 4 - 7 months. For the next 40 minutes, they feed on the old, desiccated mesocarp of these fruits by ripping open the woody pods longitudinally. No infructescence nor pod is spoiled dropping it before eaten

out completely. Particularly in this time of food scarcity, spider monkeys tend to eat very economically. At 8.00 h, all three travel back over 100 m, then the second female splits off, whereas mother and son are feeding on young leaves of a low tree. Afterwards, they rest in the middle part of the canopy for about two hours on end.

At 10.15 h, they feed shortly on young leaves of Bombax spectabile. From 10.25 - 10.35 and 10.45 - 10.55 h, they feed on the fruits of another Dimorphandra multiflora. After a short travel bout, the flowers of Guarea grandifolia are eaten for 26 minutes, broken by a rest of 15 minutes. From 11.45 - 12.15 h, mother and son travel slowly and feed on a few flowers of Bignoniaceae lianes. From 12.15 - 13.10 h, both animals rest high up in an emergent tree. When they continue their way, they meet the other female again. Some greeting vocalizations are heard, then all three feed on young leaves of Bombax spectabile, a common tree in this region but restricted to pina swamp forest along creeks. For one hour they feed without interruption on these young leaves by tearing with the teeth the apical part of the leaflets off of the costa. From 14.15 - 15.45 h, all three rest, the second female in a tree nearby. From 15.45 h on, they feed continuously for 40 minutes on the flowers of a Guarea grandifolia tree. After a rest of 20 minutes, mother and son travel to the same sleeping tree as used last night and enter the crown by leaping. The second female stays back, feeding on the flowers of a Guarea grandifolia nearby for another 10 minutes and enters the sleeping tree at 17.00 h. She sits down at the same place as last night, five meters above mother and son, who are sitting side by side. Then, the juvenile is nursed for five minutes, lying between his mothers knees. Time now is 17.15 h and the monkeys are ready to sleep, lying in forks of branches in the late afternoon sun.

Today, no long calls nor barking duets were heard and no other subgroups encountered. The observed animals feeded on a total of 14 different food plants belonging to 10 species, of which three were very important: Dimorphandra multiflora, two fruiting trees; Guarea grandifolia, three flowering trees; Bombax spectabile, young leaves of two trees. Not including the data from faeces, a total of three feeding records was made on fruits, five on flowers and six on young leaves. Total feeding time was 3½ hours of which 3 hours on the three most important species, total resting time between 6.00 - 18.45 h was 7 hours, and total travel distance was 700 m.

Comparing these two days, typical for each season, the following differences are most striking. Day range length during the long wet season can be more than six times day range during the long dry season. During the long wet season total resting time is much less and total feeding time is much more. Also the sleeping tree is left much earlier and entered much later than during the dry season. Diet composition differs strongly, much higher percentages of flowers and young leaves being eaten during the dry season. In this period, the monkeys feed very economically and activity budgets are lowered to a minimum. In general, subgroups are smaller during the long dry season and much less encounters take place with other subgroups. The monkeys are more silent.

5.2. Foraging and Feeding Techniques

5.2.1. **Foraging techniques.** In general, feeding activity within a subgroup was closely synchronized. When feeding for prolonged periods of time on the same food plant before travelling to another, usually the first feeding bout was the same for all members of the subgroup, eating at high speed. After this, short resting bouts alternated with short feeding bouts, which might not occur fully simultaneously. Juveniles spent less time in feeding than adults, filling the time remaining either playing alone, or with other juveniles and/or adults.

Mostly, the daily itineraries and the activity patterns of a subgroup were mainly determined by a dominant, mostly aged female or sometimes by two dominant females alternately. The latter occurred quite rare and over short periods of time, since both females seemed to have partly different foraging routes in mind, which resulted in several splits and joins. Because almost always, as route connecting the principal food plants was taken the shortest one possible, in geographical and ecostructural sense, and the leading female didn't often seem to hesitate, it appeared that she had, in advance, roughly mapped out in her mind the foraging route for a particular day early in the morning, while still sitting in the sleeping tree. Another indication to this remarkable behavioral pattern may be the fact that a leading female, temporarily joining another subgroup led by another female following a completely different route, could not instantaneously take up again her before planned route, just after splitting off, which apparently resulted in some inappropriate behaviour (like hin and back travelling and revisiting food plants).

When a foraging subgroup was relatively large, consisting of four or more independently locomoting animals, the monkeys tended to spread their attention over different food sources at a time, avoiding in this way possible agonistic behaviour. This type of foraging only seems to be possible when food supply is high and consequently the presence of one or more other food sources nearby is likely. During the long wet season, when this condition is fulfilled, the average subgroup size was seen to be larger.

Spider monkeys live in medium-sized, loosely associated groups fragmenting into subgroups of varying size and composition, which roam independently in the same general area. The only persistent associations are those of a female with her offspring of 0 - 4 years old. All other members of the group will join one subgroup for some time and then switch to another or go their own way. Temporary solitaries can be frequently observed, in particular during the long dry season.

This structure is a highly efficient method for the exploiting of available food sources, especially since other group members can rapidly learn of the discovery of food through conspecific cuing (Slatkin and Kiester, 1974). Since <u>Ateles</u> frequently travels and feeds in the upper part of the canopy and in emergents, at least some of this cuing is visual. Also auditory aspects may play a role, in particular through the sound produced by dropped food parts and the frequently given vocalizations while feeding. Also, after reaching a particular food source, males may give long calls or male(s) and/or female(s) may perform duet barking. The primary purpose of such activity is to pass on its location or remain in contact with other subgroups, but it may also be intended to inform kin that a food source has been located or used at the moment. On some occasions, members of other subgroups came in immediately after such vocalizations had been given.

Each dominant female appears to know part of the home range very well, here referred to as her 'core area'. Regularly, they can be observed checking food sources that will come available soon. On a number of occasions such a female was seen going off of the route in order to check a food source with unripe fruit, testing the fruit, dropping it and then returning to the rest of the subgroup. Some days, especially in the late afternoon, this behaviour could be observed , whereas the rest of the subgroup was playing or travelling already ahead towards the sleeping tree. This behaviour was not performed every day but usually at least every fourth day. In this way important food plants, approaching the edible stage, seem to be incorporated in the female's pre-planned foraging route. When this conclusion is correct, the skill of a dominant female must be of an amazing complexity, considering that the phenological picture is constantly changing and many plants are involved, dispersed over a wide area.

5.2.2. *Feeding techniques*. In the spider monkey, frugivory is characterized most strikingly by the fact that it mostly swallows the seeds of the fruit rather than discard them (Table 7).
In general, fruits are found at or near the periphery of tree crowns. Spider monkeys tend to feed by suspension and are seldom seen picking a fruit and carrying it away to a bough or branch before consuming. Fruits are picked with one hand. Many fruits are swallowed whole, but when the outer layer is tough, normally the fruit is opened with the teeth and eaten out. Few manipulation has been observed in spider monkeys feeding on fruit. This may be related to lack of a functional thumb. When fruits are very small or compound, spider monkeys may eat them after picking the whole infructescence or part of it, holding it with the hand(s) and snapping off the fruitlets directly with the mouth (e.g., in *Alchorneopsis floribunda*, *Hyeronima laxiflora*, *Pourouma* spp., *Oenocarpus bacaba*, *Guettarda acreana*). Some fruits are used only for the juice by chewing (e.g., in *Geissospermum* sp.) or only the soft outer layer is scraped off with the teeth (e.g., in *Couepia caryophylloides*, *Licania majuscula*, *Ceiba pentandra*). Manipulation of fruit parts with particular fingers has been observed rarely. Pulp and seeds of *Clusia grandiflora* are scraped with two fingers out of the locules. Pods are ripped open with the teeth along the suture(s) and eaten out, the hands holding both valves (e.g., in *Inga* spp.).
Bivalved, tardily dehiscing fruits, like of *Virola* spp., are bitten when ripe, holding the fruit with both hands. At this stage of maturity, the fruit opens easily by pressure and after pulling the valves apart with the hands or with hand and teeth, the monkey swallows both stone and aril. When predating on young seeds, spider monkeys bite out part of the fruit-wall till the seed(s) can be eaten out.

To reach some food items, like the infructescences of *Philodendron scandens* and the aerial root-tips of *Philodendron* spp., spider monkeys were observed in pulling up several meters of stem while sitting on a branch.. Once, a spider monkey sitting on a bough was seen looking down along a bunch of hanging stems of a *Philodendron scandens*, first erroneously pulling up the wrong stem and, finally, pulling up the right one and obtaining the fruiting spadix.
Breaking off branches with infructescences to feed on, like capuchin monkeys frequently do, was observed very rarely and seemed to occur rather by accident than intentionally.

The leaves selected exclusively were young leaves, as a rule occurring at the periphery of the tree crowns. Leaves could be eaten either directly or after tearing off twig or stem. Selective feeding on particular leaf parts has been observed in many cases. Parts of the lamina were ripped off of the costa with the teeth or only the apex of the leaf was bitten off. Also, young shoots and leaves still rolled up in the sheath could be preferred and sometimes the base of the petiole.

Flowers mostly occur at the periphery of crowns. Usually, flowers were eaten directly after pulling the flowering twig or stem towards the mouth or by picking them with one hand. In many cases, only the corolla was bitten off and eaten, the rest of the flower remaining attached to the peduncle, stem or twig. Sometimes, the whole inflorescence or part of it was broken off with the hand before consuming it as a whole or partly. Some species were selected only for the tips of stamens, style and/or stigma, other flowers for the sticky central body of staminodes, the honeycup or the thickened perianth.

Usually, bark eaten by spider monkeys was decaying or rotten. Almost all trees selected for this purpose apparently were healthy, but certain places, like at the edges of scars and waterholes, provided more or less decaying bark, caused by continuous contact with rain water. Frequently, the underside of boughs was selected, obviously affected by rain water regularly flowing down. Such places were quite hard to reach for the monkeys requiring much effort. Inconvenient postures had to be taken like hanging by all five extremities under a thick, horizontal bough. Many of these particular patches appeared to be used over years and their exact place apparently was known from earlier visits. It is interesting that of all 11 species of bark recorded to be eaten by the spider monkeys in the study area, 10 species were already known to them for another food item (8 for its fruit, 2 for its flush leaves). Only Nectandra cf. kunthiana was not recorded for anything else, but was never observed fruiting and it might well provide the monkey with edible fruits.

Selective feeding on bark may be important for the monkeys, since several tree species are known for its poisonous bark (e.g., Vataireopsis speciosa). Restricting bark feeding to well known species may be advantageous by limiting the chance of error. By using the same patches of certain trees traditionally, also the monkeys evade risk. Like for the observer, for the monkey different barks may be much harder to recognize individually than for instance different fruits, leaves or flowers.

Bark was eaten by biting off pieces with the teeth, gnawing for a while and ingesting the pulpy mass.

The mode of drinking out of tree holes resembles very much the behaviour of siamangs and gibbons as described by Chivers (1974) and Ellefson (1974). Water holes usually occur at the junction of branches or at sites where branches or boughs are broken off and the wood is rotten. These holes are filled with water most of the year and play an important role as water source, especially during the long dry season. The monkey would dip its hand into the hole, raise it rapidly to the mouth, uplifting the elbow to suck the water running of the back of the hand. This action sometimes could be repeated over 80 times on end. Except for tree holes, water was seen taken in the same manner from the beakers formed by the tightly imbricate leaf bases of big Bromeliads, growing epiphytic on boughs.

During the long wet season, water drinking was rarely observed, as apparently fruits, making up the main part of the diet, contain enough water.

5.3. Feeding Heights

Ateles is primarily an animal of the upper levels of the forest, where most of its food is found, especially in the periphery of crowns.

Of a total of 6105 feeding minutes, recorded for 30 days evenly spread over the year, 77.2% were passed in the upper levels of the forest, of which 22.8% in emergents (30 m or more) and 54.4% in the upper part of the canopy (25 - 30 m). The lower levels of the canopy and the understory are less important, with 16.4% in the middle part (20 - 25 m) and 5.6% in the lower part of the canopy (15 - 20 m). Ateles is rarely seen feeding in the understory (3 - 15 m), accounting for only 0.8%.

5.4. General Feeding Postures

Locomotion and postural behaviour of Ateles paniscus has been studied extensively by Mittermeier (1978), by observing the spider monkeys in the Voltzberg study area. Some of the results concerning locomotion during feeding and general feeding postures will be mentioned here shortly. For detailed description I refer to Mittermeier (1978).

Climbing, especially 'horizontal climbing', appeared to be the most important pattern during feeding. It is typified by the irregular limb

use. Most Ateles locomotion takes place on twigs and branches, with twigs playing a greater role in feeding than in travel.
Feeding postures are mainly suspensory and seated. Twigs are the most important supports in feeding postures since most of the feeding activities take place at the periphery of tree crowns.
Ateles feeding postures can be divided into three major categories: sitting, standing and suspensory. Sitting and standing postures are above branch, with the animal's weight on the support. Suspensory postures are those in which the major support is above or to the side. Most often they involve three limbs as support, the tail counting as a limb, in addition to the limbs used to grasp food.
Sitting and suspensory postures are the most important, while bipedal, tripedal and quadrupedal standing postures contribute 10 - 15%. A vertical clinging posture is occasionally used, and on rare occasions Ateles will feed from a reclining position.

5.5. **Food Selectivity**

Spider monkeys were rarely seen visiting a particular food plant more than once a day. In general, daily itineraries appeared to be formed by rational lines between sleeping trees, determined by several trees, lianes or clumps of trees, providing the monkey with food important for the moment. Only in case of subsequent use of the same sleeping tree, part of the food plants, especially those occurring nearby this sleeping tree, could be used a second time.

Usually, spider monkeys selected ripe fruits from a distance by sight. Sometimes, like in the case of **Sacoglottis cydonioides**, **Brosimum parinarioides** and **Clarisia racemosa**, the monkey would inspect the fruit by sniffing or biting it softly, since the external properties of the fruit (like colour) do not give a decisive answer on the stage of maturity.

Fruits seemed to be exploited in an optimal way. Few unripe fruits were seen picked by error and dropped. Deaf and wormy fruits often could be recognized without opening, even when they were marked only by very inconspicuous holes. Evidence has been found for the selective feeding on fruits from different trees of the same species, characterized by a better taste. For instance, spider monkeys were seen feeding only on part of the fruiting trees of the species **Spondias mombin**, available simultaneously. The selected trees turned out, without exception, to produce sweet tasting fruits, whereas the neglected ones offered bitterish tasting fruits.

As already mentioned before (Table 2), spider monkeys fed on trees in 68.1%, on lianes and stranglers in 25.6%, on twiners in 1.0% and on epiphytes in 5.3% of the total number of food plant species (n = 207).

5.6. **Temporal Patterning of Food Choice**

As an introduction to the main text on variation in food choice, I will present outlines of food choice and foraging routes performed by a spider monkey subgroup during some consecutive days in both December, 1977 and April, 1978. These months were choosen because of strikingly different availability of preferred food. Besides, both periods of observation were selected since a particular dominant female with her juvenile son was observed continuously, and found fully to determine the ranging behaviour of all individuals joining 'her' subgroup during observation time.

Ateles day ranges appeared to be mainly determined by several food plants, here referred to as 'primary food sources'. Usually, these sources produce large, relatively fast-ripening (or in the case of leaves, shortly flushing) crops, enough for all members of a subgroup to feed on together. Normally, feeding bouts are relatively long in this category. Most of these sources are common, occurring throughout the home range, but some years crops can fail. Examples of this category are: *Virola melinonii*, *Ecclinusa guianensis*, *Achrouteria pomifera*, *Tetragastris* spp., *Protium* spp., *Ceiba pentandra* and *Guarea grandifolia*.

'Secondary food sources' are called those producing smaller, slow-ripening crops, available for prolonged periods, but at any moment offering more than one or two animals too little to make a meal, e.g., *Strychnos tomentosa*, *Pereskia aculeata*, *Eschweilera* spp., *Paullinia sphaerocarpa*, *Cecropia sciadophylla*, *Coussapoa asperifolia*, *Leretia* sp., *Carapa procera* (young seeds), *Philodendron* spp. (infructescences) and *Hylocereus* spp. (infructescences). These food sources will be used only by one or two members of a subgroup on its way from one 'primary food source' to another. Normally, feeding bouts are short.

'Tertiary food sources' are defined as reliable sources available for prolonged periods of time, sometimes for several months or even longer. Usually, these sources occur throughout the home range and may be either used by all members of a subgroup or part of it on the way from one 'primary food source' to another. Feeding bouts vary, but may be long. Examples of this category are:
Dimorphandra multiflora (desiccated fruit), *Carapa procera* (leaves), *Peperomia glabella* (shoots), *Philodendron* spp. (leaves, shoots and aerial roots), *Norantea guianensis* (flowers), *Licania micrantha* (bark), *Hylocereus* spp. (flowers), *Bellucia grossularioides* (fruit), *Eperua falcata* (leaves) and *Pterocarpus officinalis* (leaves). Crops of 'tertiary food sources' rarely fail and the monkey can depend on them every year.

In Tables 9 and 10, all food species and food items, used by a spider monkey subgroup during four consecutive days in both December, 1977 and April, 1978, are listed, the amount of feeding time for each has been indicated and the category to which each food source belongs. The corresponding daily itineraries of the subgroup are mapped in Figs. 24 - 27, with the food sources used indicated by the number in the day's list in Tables 9 and 10.

During four consecutive days of observation in December, 'primary food sources' accounted for 87.7% of total feeding time, whereas feeding on 'secondary' and 'tertiary' food sources made up only 1.2% and 11.1% resp. During four consecutive days of observation in April, 'primary food sources' accounted for 89.7% of total feeding time, whereas feeding on 'secondary' and 'tertiary' food sources only made up 8.1% and 2.2% resp.

Table 9. Food choice of a spider monkey subgroup during several days in December, 1977. The numbers of the food plants used correspond with those on the map (Figs. 24 and 25). Also, food item and feeding time are listed

December, 2			
1.	Hymenolobium flavum	sleeping tree	
2.	Bagassa guianensis	infructescence	74 min.
3.	Brosimum parinarioides	infructescence	117 ,,
4.	Inga pezizifera	pods checked, not ripe yet	
5.	Philodendron acutatum	young leaves, shoots	3 ,,
6a.	Philodendron scandens	shoots	4 ,,
b.	Coussapoa latifolia	infructescence	4 ,,
7a.	Philodendron acutatum	aerial root-tips	3 ,,
b.	Paullinia sphaerocarpa	young seeds	1 ,,
8.	Inga sp.	pods checked, not ripe yet	
9a.	Eschweilera congestiflora	young seeds + aril	3 ,,
b.	Hillia illustris	flowers	2 ,,

Table 9 (continued)

10.	Philodendron acutatum	aerial root-tips	2 min.
11.	Sacoglottis cydonioides	bark	2 ,,
12.	Inga alba	bark	2 ,,
13a.	Not ident. sp. (Gesneriaceae)	young leaves	11 ,,
b.	Tabebuia serratifolia	young leaves	12 ,,
14.	Achrouteria pomifera	fruit	41 ,,
15.	Couratari stellata	bark	2 ,,
16.	Ceiba pentandra	young leaves	8 ,,
17.	Couratari stellata	sleeping tree	
18.	Vochysia tomentosa	sleeping tree	

Weather: sunny; heavy rain from 14.36 - 15.00 and 17.00 - 19.00 h
Observation time: 5.48 - 17.00 h Day range size: 1500 m
Total food spp. used: 16 Total food items used: 18
Total feeding time: 308 minutes
on primary food sources (no. 2,3,6b,14,16) - - - - - - - - 244 min.
on secondary food sources (no. 7b,9) - - - - - - - - - - - - 6 ,,
on tertiary food sources (no. 5,6a,7a,10,11,12,13,15) - - - 41 ,,
Most important food spp. calculated in feeding time: Brosimum parinarioides (117 min.), Bagassa guianensis (74 min.), Achrouteria pomifera (41 min.)
Subgroup size and composition: 5.48 - 13.38 h - 4 (2 ♀♀, 1 ♂, 1 juv.3♂)
13.38 - 17.00 h - 7 (+ 2 ♀♀, 1 inf.1)

- -

December, 3

1.	Cecropia sciadophylla	infructescence	5 min.
2.	Cecropia sciadophylla	infructescence	2 ,,
3.	Bagassa guianensis	infructescence	17 ,,
4.	Pouteria sp. (400)	young seeds	8 ,,
5.	Vataireopsis speciosa	young leaves	3 ,,
6.	Bagassa guianensis	infructescence	9 ,,
7a.	Peperomia glabella	shoots	3 ,,
b.	Ficus americana	figs	94 ,,
c.	Ceiba pentandra	young leaves	3 ,,
8.	Xylophragma seemannianum	flowers	3 ,,

Weather: sunny; heavy rain from 11.25 - 12.00 and 12.07 - 12.35 h
Observation time: 5.40 - 13.00 h, then lost contact
Day range size: 900 + 1600 m (hypothetic)
Total feeding time: 147 minutes
on primary food sources (no. 3,5,6,7b,7c,8) - - - - - - - 129 min.
on secondary food sources (no. 1,2,4) - - - - - - - - - - - 15 ,,
on tertiary food sources (no. 7a)- - - - - - - - - - - - - 3 ,,
Most important food spp. calculated in feeding time: Ficus americana (94 min.), Bagassa guianensis (26 min.)
Subgroup size and composition: 5.40 - 8.50 h - 4 (2♀♀, 1♂, 1juv.3♂)
8.50 -13.00 h - 3 (1♀ left subgroup)

- -

December, 4

1.	Hymenolobium flavum	sleeping tree	
2.	Bagassa guianensis	infructescence	29 min.
3.	Brosimum parinarioides	infructescence	32 ,,
4.	Bellucia grossularioides	fruit	11 ,,
5.	Ampelocera edentula	young leaves	1 ,,
6.	Sacoglottis cydonioides	bark	1 ,,
7.	Trichilia quadrijuga	fruit	18 ,,

Table 9 (continued)

8.	Dimorphandra multiflora	fruit	10 min.
9.	Leretia sp.	fruit	5 ,,
10.	Achrouteria pomifera	fruit	10 ,,
11.	Xylophragma seemannianum	flowers	8 ,,
12.	Coussapoa asperifolia	infructescence	2 ,,
13.	Cordia sagotii	fruit	5 ,,
14.	Achrouteria pomifera	fruit	4 ,,
15.	Clarisia racemosa	fruit	5 ,,
16.	Ceiba pentandra	young leaves	37 ,,
17.	Inga leiocalycina	bark	5 ,,
18.	Guatteria chrysopetala	fruit	12 ,,
19.	Achrouteria pomifera	fruit	6 ,,
20.	Dimorphandra multiflora	fruit	9 ,,
15.	Clarisia racemosa	fruit	8 ,,
21.	Licaria cayennensis	young leaves	4 ,,
22.	Apeiba echinata	flowers	1 ,,
23.	Xylophragma seemannianum	flowers	4 ,,
	in Couratari guianensis	sleeping tree	

Weather: sunny; heavy rain from 16.45 - 19.30 h
Observation time: 5.40 - 16.45 h Day range size: 1250 m
Total food spp. used: 18 Total food items used: 18
Total feeding time: 227 minutes
on primary food sources (no.2,3,7,10,11,13,14,15,16,18,19,23)-178 min.
on secondary food sources (no. 9,12) - - - - - - - - - - - - - - - 7 ,,
on tertiary food sources (no. 4,5,6,8,17,20,21,22)- - - - - - - 42 ,,
Most important food spp. calculated in feeding time: Ceiba pentandra (37 min.), Brosimum parinarioides (32 min.), Bagassa guianensis (29 min.) Achrouteria pomifera (20 min.), Dimorphandra multiflora (19 min.), Trichilia quadrijuga (18 min.)
Subgroup size and composition: 5.40 - 12.15 h - 6 (3♀♀, 1♂, 1juv.2♀, 1juv.3♂)
12.15 - 16.45 h - 3 (2♀♀, 1juv.2♀)

- -

December, 5

1.	Vataireopsis speciosa	sleeping tree + young leaves	55 min.
2.	Vochysia tomentosa	sleeping tree (old male only)	
16.	Ceiba pentandra	young leaves	41 ,,
3.	Achrouteria pomifera	fruit	33 ,,
4.	water		
10.	Achrouteria pomifera	fruit	18 ,,
5.	Bagassa guianensis	infructescence	16 ,,
5.	Ampelocera edentula	young leaves	2 ,,
4.	Bellucia grossularioides	fruit	10 ,,
2.	Bagassa guianensis	infructescence	35 ,,
1.	Hymenolobium flavum	sleeping tree	

Weather: sunny; heavy rain from 11.35 - 11.50, 13.48 - 14.37 and 17.15 - 18.45 h
Observation time: 5.45 - 17.10 h Day range size: 850 m
Total food spp. used: 6 Total food items used: 6
Total feeding time: 210 minutes
on primary food sources (no. 1,2,3,5,10,16)- - - - - - - - 198 min.
on secondary food souces - - - - - - - - - - - - - - - - - - 0 ,,
on tertiary food sources (no. 4,5) - - - - -
Most important food spp. calculated in feeding time: Vataireopsis speciosa (55 min.), Bagassa guianensis + Achrouteria pomifera (51 min.), Ceiba pentandra (41 min.)
Subgroup size and composition: 3 (1♀, 1♂, 1juv.3♂)

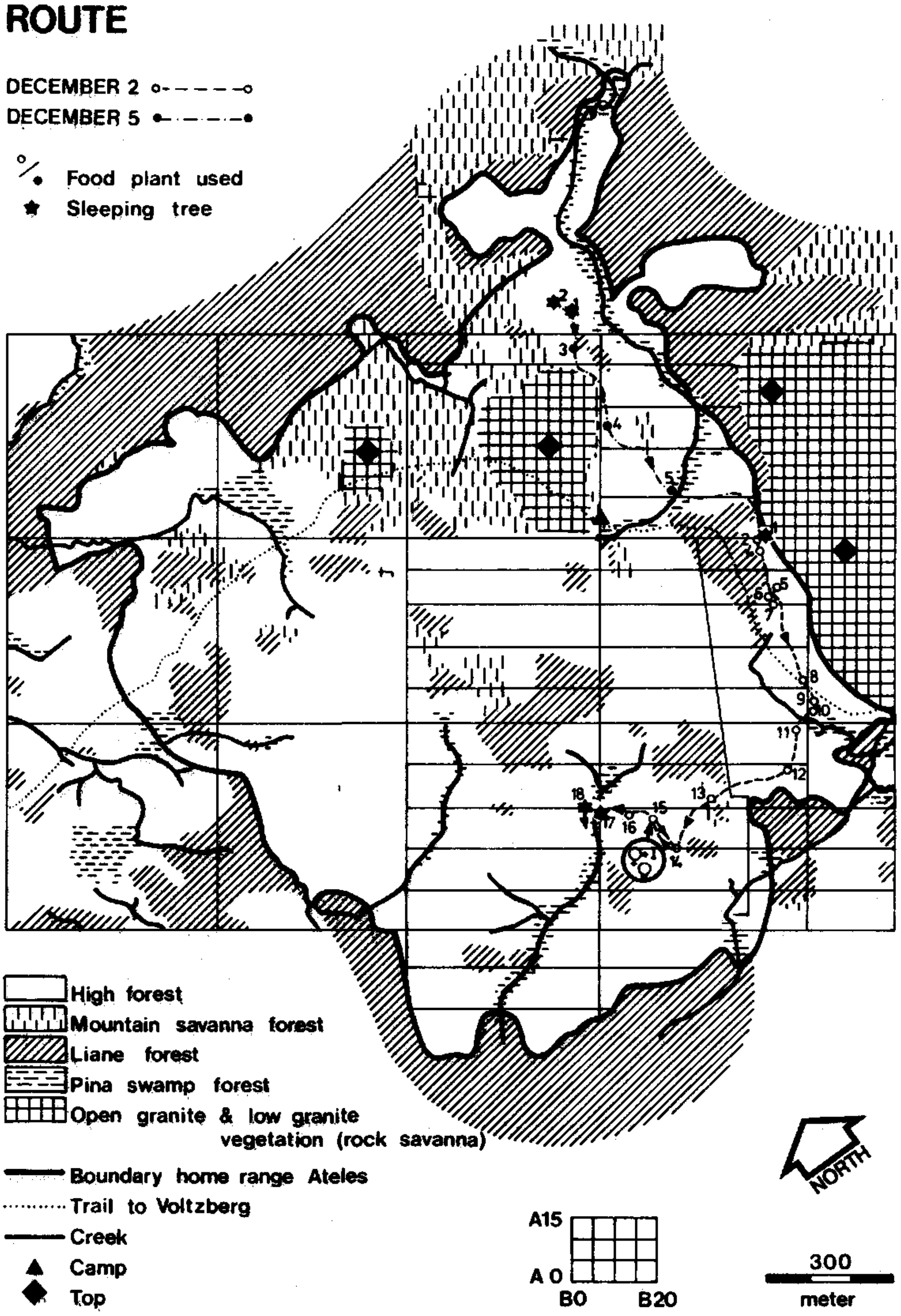


Fig. 24. Route followed by a spider monkey subgroup both on December 2 and 5, 1977. The numbers of the food plants and sleeping trees used correspond with those of Table 9.

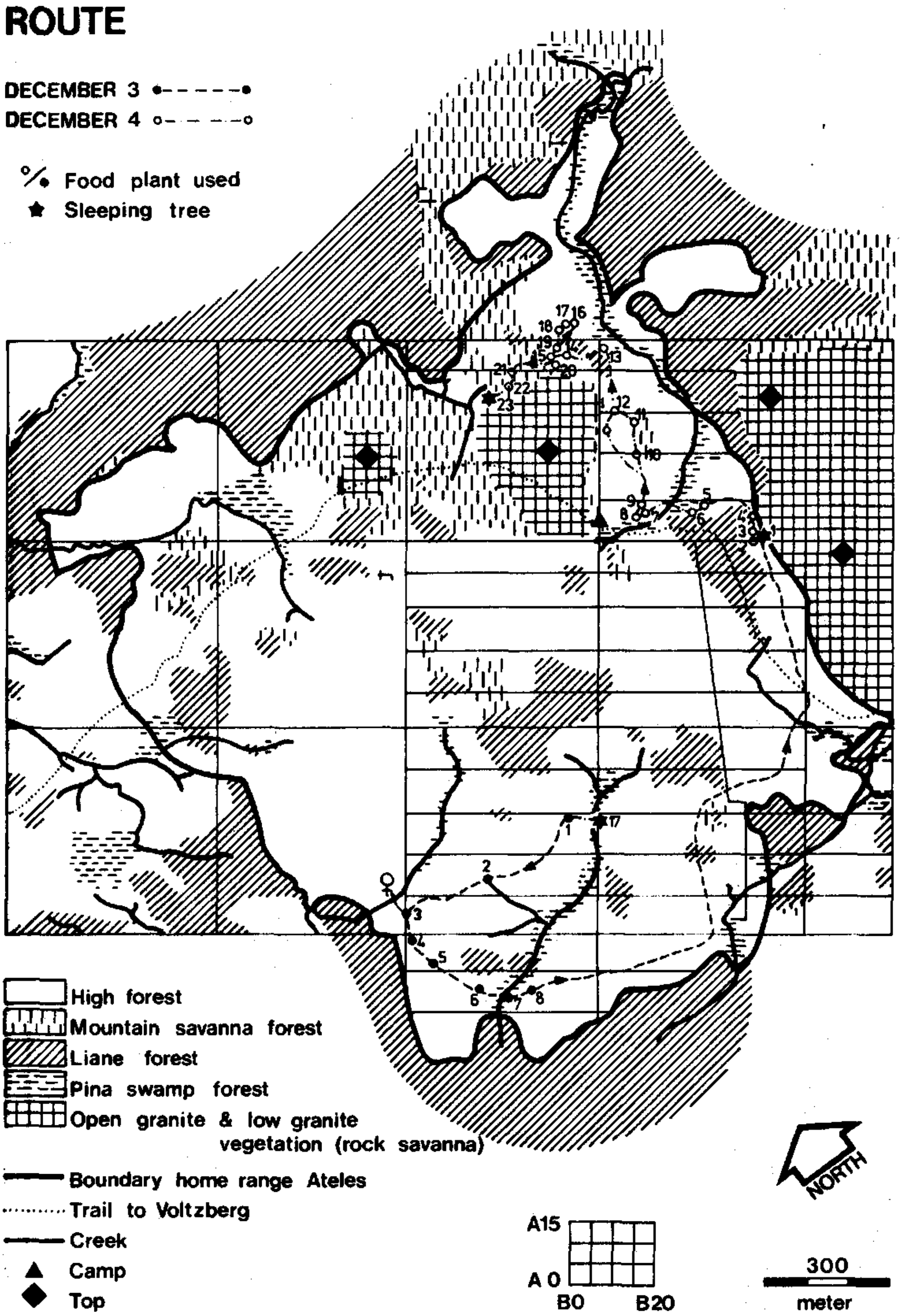


Fig. 25. Route followed by a spider monkey subgroup both on December 3 and 4, 1977. The numbers of the food plants and sleeping trees used correspond with those of Table 9.

Table 10. Food choice of a spider monkey subgroup during several days in April, 1978. The numbers of the food plants used correspond with those on the map (Figs. 26 and 27). Also, food item and feeding time are listed

---

April, 23

1.	Hymenolobium flavum	sleeping tree	
2.	Tetragastris altissima	fruit	9 min.
3.	Tetragastris panamensis	fruit	25 ,,
4.	Tetragastris panamensis	fruit	39 ,,
5.	Styrax cf. fanshawei	fruit	28 ,,
	water		
6.	Cecropia sciadophylla	infructescence	14 ,,
7.	Ecclinusa sp.	fruit	4 ,,
8.	Cayaponia ophthalmica	fruit	2 ,,
9.	Guettarda acreana	fruit	4 ,,
10.	Sterculia excelsa	young seeds	2 ,,
11.	Cecropia sciadophylla	infructescence	1 ,,
12.	Coussarea paniculata	fruit	1 ,,
13.	Geissospermum sp.	fruit (juice)	7 ,,
14.	Rheedia macrophylla	fruit	7 ,,
15.	Guarea grandifolia	fruit	9 ,,
16.	Geissospermum sp.	fruit (juice)	5 ,,
17.	Not ident. liane	young leaves	4 ,,
18.	Ecclinusa sp.	fruit	10 ,,
19.	termites in Hymenolobium flavum		4 ,,
20.	Cecropia sciadophylla	infructescence	6 ,,
21.	Hymenolobium flavum with Philodendron acutatum	sleeping tree young leaves	2 ,,

<u>Weather</u>: sunny; no rain

<u>Observation time</u>; 10.25 - 18.20 h — <u>Day range size</u>: 1900 m

<u>Total food spp. used</u>: 15 — <u>Total food items used</u>: 15

<u>Total feeding time</u>: 183 minutes
on primary food sources (no. 2,3,4,5,7,9,13,15,16,18) - - 140 min.
on secondary food sources (no. 6,8,10,11,12,14,20) - - - - 33 ,,
on tertiary food sources (no. 17,19,21) - - - - - - - - - - 10 ,,

<u>Most important food spp. calculated in feeding time</u>: Tetragastris panamensis (64 min.), Styrax cf. fanshawei (28 min.), Tetragastris altissima (25 min.), Cecropia sciadophylla (21 min.)

<u>Subgroup size and composition</u>: 10.25 - 17.00 h - 6 (3♀♀, 1juv.3, 1inf.1)
after 17.00 h - 7 (old ♂ joined subgr.)

- -

April, 24

21.	Hymenolobium flavum	sleeping tree	
2.	Tetragastris altissima	fruit	69 min.
1.	Clusia scrobiculata	fruit	6 ,,
3.	Tetragastris panamensis	fruit	2 ,,
4.	Tetragastris panamensis	fruit	44 ,,
5.	Guarea grandifolia	fruit	1 ,,
6.	Mendoncia hoffmannseggiana	fruit	15 ,,
7.	Guarea grandifolia	fruit	13 ,,
8.	Not ident. liane (Celastraceae)	fruit	8 ,,
9.	Cayaponia rigida	fruit	16 ,,
10.	Guarea grandifolia	fruit	6 ,,
11.	Guarea grandifolia	fruit	35 ,,
	water in Caraipa sp.		

Table 10 (continued)

12. Guarea grandifolia	fruit	9 min.
13. Guarea grandifolia	fruit	4 ,,
14. Moutabea guianensis	fruit	4 ,,
15. Strychnos tomentosa	fruit	3 ,,
16. Inga alba	bark	6 ,,
17. Strychnos tomentosa water in Inga alba	fruit	6 ,,
18. Guarea grandifolia	fruit	4 ,,
19. Inga alba	bark	4 ,,
20. Guarea grandifolia	fruit	4 ,,
21. Spondias mombin	fruit	15 ,,
22. Guarea grandifolia	fruit	15 ,,
23. Vochysia tomentosa	sleeping tree	

Weather: sunny; no rain
Observation time: 5.40 - 18.10 h Day range size: 2680 m
Total food spp. used: 11 Total food items used:11
Total feeding time: 291 minutes
on primary food sources (no. 2,3,4,5,6,7,8,9,10,11,12,13, 18,20,21,22) -262 min.
on secondary food sources (no. 1,14,15,17) - - - - - - - - - - 19 ,,
on tertiary food sources (no. 16,19) - - - - - - - - - - - - 10 ,,
Most important food spp. calculated in feeding time: Guarea grandifolia (91 min.), Tetragastris altissima (69 min.), Tetragastris panamensis (46 min.)
Subgroup size and composition: 5 (2♀♀, 1♂, 1juv.3♂, 1inf.1)
from 14.20 - 16.20 h - 3 (♀ + inf. lost contact and joined again)

- -

April, 25

23. Hymenolobium flavum	sleeping tree	
1. Guarea grandifolia	fruit	7 min.
2. Tetragastris altissima	fruit	16 ,,
3. Tetragastris panamensis	fruit	16 ,,
4. Ficus trigonata	figs	2 ,,
5. Clusia scrobiculata	fruit	3 ,,
6. Tetragastris panamensis	fruit	9 ,,
7. Guarea grandifolia	fruit	6 ,,
8. Tetragastris panamensis	fruit	2 ,,
9/6. Cecropia sciadophylla	infructescence	6 ,,
10/5. Styrax cf. fanshawei	fruit	14 ,,
11/3. Tetragastris panamensis	fruit	3 ,,
12/2. Tetragastris altissima	fruit	29 ,,
13. Bombax spectabile	young seeds	1 ,,
12. Tetragastris altissima	fruit	41 ,,
11. Tetragastris panamensis	fruit	4 ,,
14. Ficus pertusa	figs	9 ,,
15. Philodendron sp.	infructescence	6 ,,
16. Bombax spectabile	flowers	2 ,,
17. Guarea grandifolia	fruit	12 ,,
18. Guarea grandifolia	fruit	12 ,,
19. Geissospermum sp.	fruit (juice)	15 ,,
20. Guarea grandifolia	fruit	5 ,,
21. Inga alba	bark	1 ,,
22. Inga bourgoni	fruit	8 ,,
23. Moutabea guianensis	fruit	3 ,,
24. Spondias mombin	fruit	13 ,,

Table 10 (continued)

19.	Geissospermum sp.	fruit	8 min.
17.	Guarea grandifolia	fruit	2 ,,
20.	Guarea grandifolia	fruit	4 ,,
25.	Guarea grandifolia	fruit	4 ,,
26.	Guarea grandifolia	fruit	1 ,,
27.	Guarea grandifolia	fruit	3 ,,
12/2.	Tetragastris altissima	fruit	95 ,,
28.	Guarea grandifolia	fruit	3 ,,
1.	Hymenolobium flavum	sleeping tree	

Weather: sunny; heavy rain from 13.54 - 14.04, 14.20 - 14.35, and 18.05 - 18.25 h

Observation time: 5.35 - 17.35 h Day range size: 2850 m

Total food spp. used: 15 Total food items used: 16

Total feeding time: 365 minutes

on primary food sources (no. 1,2,3,4,6,7,8,10,11,12,14, 17,18,19,20,22,24,25,26,27,28)- 343 min.

on secondary food sources (no. 5,9,13,15,16,23) - - - - - 21 ,,

on tertiary food sources (no. 21) - - - - - - - - - - - 1 ,,

Most important food spp. calculated in feeding time: Tetragastris altissima (181 min.), Guarea grandifolia (59 min.), Tetragastris panamensis (34 min.), Geissospermum sp. (23 min.)

Subgroup size and composition: 5.35 - 8.00 h - 5 (2♀♀, 1o, 1juv.3o)
8.00 -17.30 h - 7 (1♀ + 1juv.2♀ joined)

- -

April, 26

1.	Hymenolobium flavum	sleeping tree	
2.	Guarea grandifolia	fruit	4 min.
3.	Cayaponia rigida	fruit	7 ,,
	Inga edulis	pods checked only	
4.	Virola surinamensis	fruit	25 ,,
5.	Clusia grandiflora	fruit	2 ,,
6.	Clusia grandiflora	fruit	1 ,,
7.	Guarea grandifolia	fruit	1 ,,
8.	Tetragastris panamensis	fruit	5 ,,
9.	Spondias mombin	fruit	11 ,,
10.	Tetragastris panamensis	fruit	6 ,,
11.	Tetragastris panamensis	fruit	6 ,,
12.	Tetragastris altissima	fruit	5 ,,
13.	Guarea grandifolia	fruit	8 ,,
14.	Bagassa guianensis	infructescence	7 ,,
15/21.	Spondias mombin	fruit	12 ,,

Weather: rainy all day (from 6.05 h)

Observation time: 5.45 - 9.10 h and 12.36 - 13.30 h

Total feeding time: 100 minutes

on primary food sources (no. 2,3,4,7,8,9,10,11,12,13, 14,15) - - 97 min.

on secondary food sources (no. 5,6) - - - - - - - - - - - 3 ,,

on tertiary food sources - - - - - - - - - - - - - - - - - - 0 ,,

Most important food spp. calculated in feeding time: Virola surinamensis (25 min.), Spondias mombin (23 min.), Tetragastris panamensis (17 min.), Guarea grandifolia (13 min.)

Subgroup size and composition: 5.45 - 9.10 h - 5 (2♀♀, 1o, 1juv3o)
12.36 - 13.30 h - 7 (1♀ + 1juv.2♀ joined)

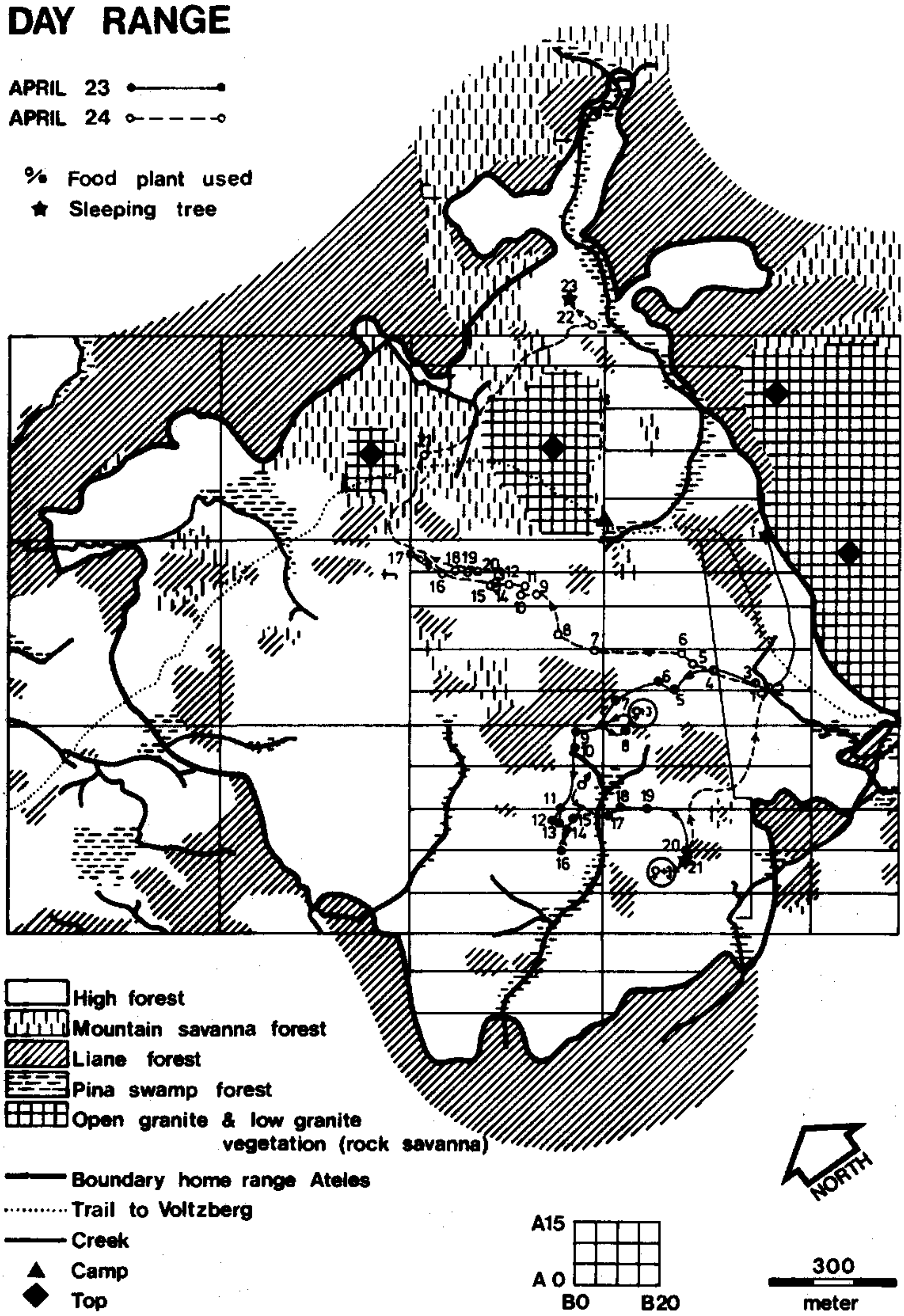


Fig. 26. Route followed by a spider monkey subgroup both on April 23 and 24, 1978. The numbers of the food plants and sleeping trees used correspond with those of Table 10.

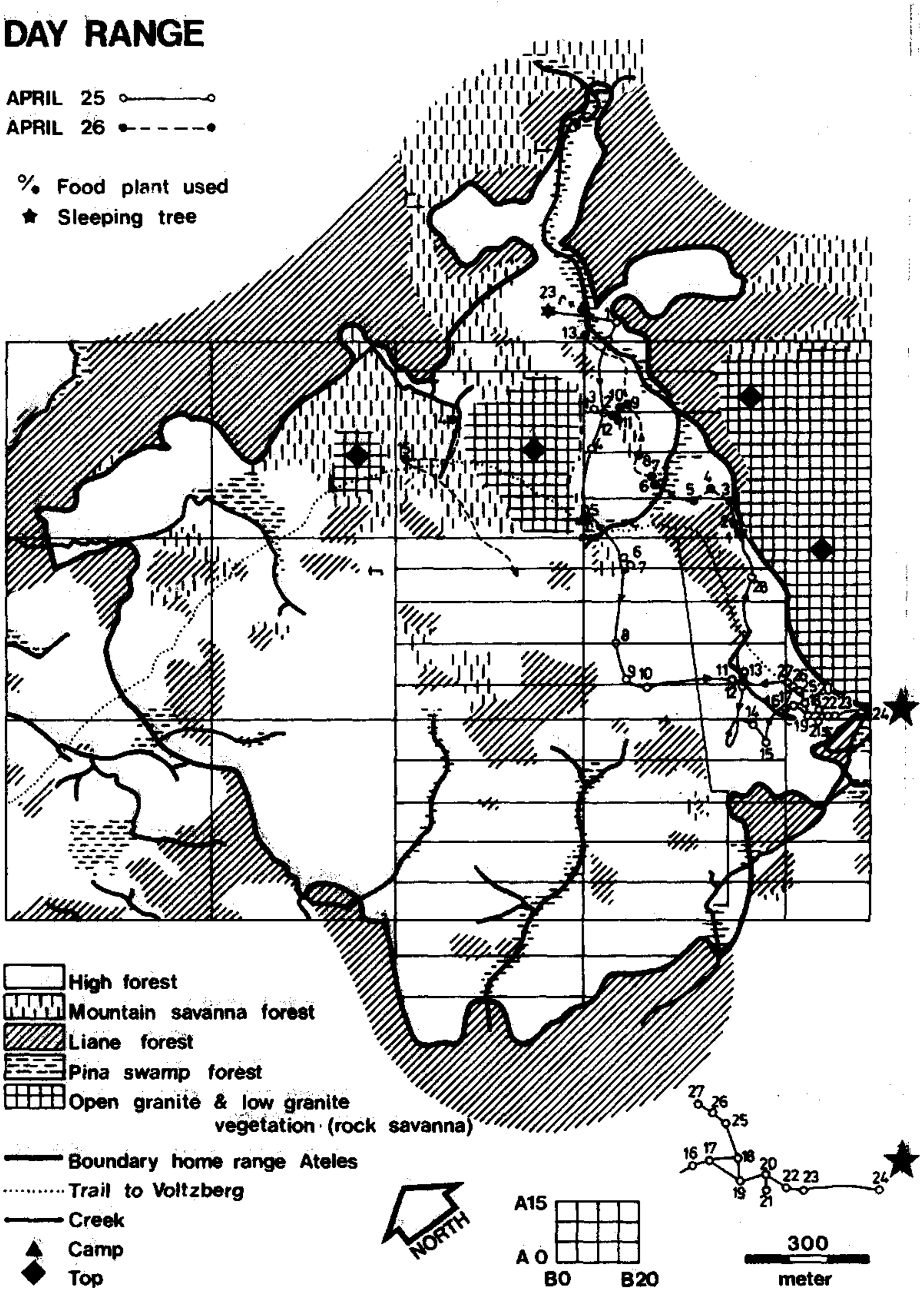


Fig. 27. Route followed by a spider monkey subgroup both on April 25 and 26, 1978. The numbers of the food plants and sleeping trees used correspond with those of Table 10.

5.6.1. Diurnal variation in food choice. Spider monkeys appeared to select for variety of food. As shown in Tables 9 and 10, a spider monkey subgroup used on average 14 different food items each day, both in December and April, representing only about a quarter of the total monthly number (Figs. 15 and 23). Of these, 3 or 4 food items were most important considering the amount of feeding time and the estimated total weight of food ingested. Duration of feeding visits to these 3 or 4 mainly 'primary' food sources could be long but never exceeded two hours. Most feeding visits to other food sources were short, ranging between 1 - 15 minutes.

Daily patterns of food use could be recognized. Fruits were eaten throughout the day, but usually two feeding peaks occurred, early in the morning and late in the afternoon. A third peak might occur around midday (between 11.00 - 13.00 h) (Van Roosmalen, in prep.).

Leaf-eating occurred throughout the day in the period July - January, and increased during the course of the day, but from January - July it occurred mainly in the late afternoon. This pattern may be explained as follows. Fruit-eating requires more energy expenditure during suspensory behaviour in the periphery of crowns than leaf-eating. When fruits are abundant (from January - July) and activity budgets correspondingly are high, it seems likely that the monkeys prefer to leave the easy eating of young leaves (e.g., proteins) for the late afternoon, when they are more tired. On the other hand, increase of leaf-eating in spider monkeys is correlated strongly with decrease in extent and rate of ranging (for example, see Table 9, December, 5).

Feeding on flowers occurred throughout the day in the period July - January, and increased during the course of the day in January and February. Flowers of Bignoniaceae and Cactaceae (e.g., Hylocereus), however, were consumed especially in the morning, when the corolla had just opened.

Feeding on bark and palm sheaths was more frequently observed during the morning, with a peak between 10.00 - 12.00 h.

The consumption of other food items, like honey, insects, aerial roots and pseudobulbs, occurred infrequently throughout the day, and sample size is too small for determining possible general patterns.

5.6.2. Variation in food choice between days. Diet changed considerably from day to day. Spider monkeys usually exploited the food sources of a particular part of the home range in a 2 - 4 days cycle.

The cycling pattern shifted constantly at variable rate, depending on the kind and the availability of present food sources. In general, 'primary food sources', which predominantly determine the cycling pattern, are ripening or flushing over short periods. Some of these sources provide the whole subgroup enough to feed on day after day.

If not exploited by the monkeys, the mature fruits c.q. infructescences either open their valves and become available to birds (e.g., Virola spp., Laetia procera, Tetragastris spp.) or drop to the ground (e.g., Bagassa guianensis, Brosimum parinarioides). Consequently, when such a preferred food source becomes available, a spider monkey subgroup almost every day will include it in its itinerary (Table 9, e.g., Bagassa guianensis, no. 2 and Brosimum parinarioides, no. 3; Table 10, e.g., Tetragastris altissima, no. 12 and Tetragastris panamensis, no. 3).

In this way, these particular food sources may play a central role in daily ranging behaviour for some time. Most 'primary food sources', however, do not have dehiscent fruit nor spill a fruit crop in a short period of abundance, but produce mature fruit more gradually. Food sources of the latter category may be visited once in 2 - 4 days (e.g., Styrax cf. fanshawei, Spondias mombin, Inga spp.). In the meantime, enough fruits can ripen and become available for the whole subgroup to feed on at a next visit. Solitary ranging animals may visit some of these sources in between the visits of a larger subgroup led by a dominant female, but the relatively small amount of food eaten by them may not thwart the pattern.

Dominant females, usually leading a subgroup, each tend to exploit different parts of the home range, except when a fruit excess occurs. This pattern is shown in Tables 9 and 10. Only two females, belonging to that part of the group followed over days both in December and April, were dominant females, each accompanied by a juvenile child and leading a subgroup mostly containing a male and/or one or more females (with or without offspring). During the days of observation in December, a period relatively scarce in preferred fruit, both dominant females rarely joined their subgroups and obviously exploited partly different areas of the home range. In April, both females frequently joined their subgroups, following about the same itineraries, but feeding on partly different food sources, a pattern made possible by the excess of preferred fruit.

In general, 'secondary food sources', which usually ripen slowly, are not visited more than once in two days. Most intervals between feeding visits appeared to be even longer, often ranging from 4 - 8 days or more, depending on the food species. 'Tertiary food sources' usually produce enough for short feeding visits every day, but since most of these food sources are not really preferred by the monkey and occur throughout the home range, they do not clearly affect daily ranging pattern. However, some 'tertiary food sources' may be important, particularly during the long dry season, when a food scarcity exists. Except for several 'primary food sources', some 'tertiary food sources', like Dimorphandra multiflora (the old fruits offering desiccated mesocarp over long periods of time) and Bellucia grossularioides (producing fruit almost continuously), may affect or even determine daily ranging pattern during the long dry season. In these cases, intervals between feeding visits may be as short as one day.

'Primary' and 'tertiary' food sources may also be revisited next day when the monkeys take a 'day-off'. This may happen after a period or in between two periods of intensive foraging in order to check new areas for food becoming available. Two or three days with large day ranges are followed by one or two days with small day ranges, determined only by few food sources which are exploited more extensively (e.g., Table 9, December, 5).

6. DIET, FEEDING STRATEGY AND SOCIAL ORGANIZATION

6.1. Introduction

The social organization of spider monkeys is quite unusual among primates and by now only for the chimpanzee (Pan troglodytes) a somewhat similar system has been found (Azuma and Toyoshima, 1962; Reynolds and Reynolds, 1965; Goodall, 1973; Sugiyama, 1973; Bygott, 1974; Wrangham, 1975). The similarities between spider monkey and chimpanzee social organization will be discussed later in this chapter.

Spider monkeys live in social groups or communities, defined by Klein and Klein (1975) as 'a network of animals that usually interact peacefully with one another'. These groups are separated from one another by agonistic interactions, according to my observations conducted mainly by the males by means of calling behaviour, with considerable distance between distance between the opposing animals. Thus, they appeared to act territorial and to respect quite clearcut boundaries.

Very occasionally, a sort of boundary conflict was observed which was initiated by one or more males near the boundary with very agitated long calling and barking, causing a rush of nearby subgroups towards the spot. At these rare incidents, it was not possible to observe individuals of both groups at the same time because of the distance between the opponents, but probably also visual contact took place between both high up in the canopy. I never observed really attacking males of different groups.

Females normally stay within the boundaries of a group's range but occasionally do visit members of neighbouring groups for periods ranging from several hours to about one day, while sometimes even staying overnight with members of neighbouring groups. These visits especially appeared to be undertaken by females with newborn infants, and if so, they seemed to be intended to show the infant to the neighbouring group. Several members of the resident group were seen grouping around mother and infant, touching and sniffing it carefully. During these visits, I never observed agonistic behaviour by any member of the resident group towards the visitors. Once, in the late afternoon, two females and a male juvenile-3 were followed over more than one kilometer outside the home range, where they contacted some members of the neighbouring group staying overnight with them. The trip was initiated by the dominant female after hearing a male repeatedly giving long calls far away. When crossing the home range boundary, they left behind another female with juvenile and a male, till then belonging to the same subgroup. In this particular case no newborn infant was involved, and the behaviour may be explained as visiting one or more relatives. Some indications have been found that sometimes emigration may take place, especially in the case of young females.

6.2. Group Size and Group Composition

One of the most striking characteristics of spider monkey social organization appears to be that never all members belonging to a certain group can be observed together at the same place. At the end of the field period, the study group consisted of 18 animals: 3 adult males, 8 adult females, 1 subadult female, 4 juveniles (2♂♂ and 2♀♀), and 2 infants (1♂ and 1♀).
The largest subgroup ever observed in the study group counted 9 individuals: once 3 males, 4 females and 2 juveniles, another time 2 males, 4 females and 3 juveniles. Two other groups that were regularly encountered in the Raleighvallen-Voltzberg Reserve counted 15 - 20 individuals, of which 3 - 4 were adult males. The overall impression is that the study group can be regarded as an average group according to group size and group composition.

6.3. Social Organization

6.3.1. Grouping behaviour.

Members of a spider monkey group associate in temporary *subgroups* or *parties* of changing composition. As criterion for individuals to belong to a subgroup or party, mutually interdependent actions in feeding and travelling were used. A female, for instance, that often travelled about 50 m behind a subgroup consisting of at least a certain male, female and juvenile, as result of regular agonistic behaviour of the male (in particular when feeding on the same food source), was considered to belong to the subgroup. Also, when a party split but obviously keeping visual and/or auditory contact between both subparties while travelling from one food source to another, following slightly different routes, all animals were considered to belong to one subgroup for that time. But when a party split and the 'subparties' followed different foraging routes and used different food sources without keeping visual or auditory contact and somewhat later joined again in a mostly primary food source, both 'subparties' were considered temporary subgroups for that time.

6.3.2. Female dominance. As stated before, within a group of spider monkeys several females easily can be recognized as dominant females, leading a subgroup and determining daily itineraries and activity patterns of the subgroup as a whole. These females appear to possess the best knowledge of available food sources within certain parts of the home range, here referred to as 'core areas'. To this end, they follow the constantly changing phenological picture by frequently checking the different food plants on the stage of flushing, flowering, or fruiting. Regularly, in particular during the late afternoon, dominant females were observed checking certain food sources becoming available in order to incorporate them into the itineraries of following days or weeks. The rest of the subgroup, associated with this female, already travelled towards a sleeping tree or a well-known food source nearby. When the dominant female was accompanied by a juvenile child, it might join her, or play in the meantime with another juvenile or adult of the subgroup, or stick to the travelling part of the subgroup.
Figures 28, 29 and 30 show the pattern of temporary associations with a certain dominant female, leading the frequently changing subgroup, on consecutive days (February 11,12,13,15,16,17 and 18, 1978).

The route taken by a dominant female usually appeared to be preplanned and highly economic, using the shortest possible connections between subsequent food sources (as shown in Figs. 28,29 and 30). Double-backing was rare and, if it occurred, it seemed to be caused by confusion, for instance after meeting and shortly assembling to another subgroup, that followed a route determined by the other leading female. When mapping day ranges of solitary males or non-dominant females, it is obvious that they are incapable in preplanning an economic route without at least making some loops, using certain important and well-known food sources more than once a day (Fig. 31). Also, their knowledge of the available food sources and their exact location appeared to be much poorer, resulting in a less varied diet composed mainly of particular food sources well-known to most members of the group, as long as they were not associated with a subgroup led by a dominant female. For males and non-dominant females it will be advantageous to join dominant-female subgroups to learn by conspecific cuing (Slatkin and Kiester, 1974) about the available food sources of the moment.

In total, four dominant females could be recognized in the study group, of which three were permanently accompanied by a juvenile child at the end of the field period. Most observations were made of a female with a male juvenile-3 and a female with a female juvenile-2, using partly overlapping core areas most of the year, with the camp situated about in the center. The combined core area roughly was situated between B8 and B20 (Fig. 32). Except for the two dominant females with juvenile, two males and two non-dominant females without offspring were encountered most frequently in this area.

In Table 11, monthly association patterns between and with both dominant females are given by calculating the percentage of total observation time for four categories of subgroup composition: 1) no dominant female(s) belonging to the subgroup 2) one dominant female belonging to the subgroup 3) both dominant females belonging to the subgroup, and 4) at least one dominant female belonging to the subgroup.
For this purpose, juveniles are considered unities with their mother, forming a strong bond and only rarely separating shortly from one another. Thus, in these calculations six adults are involved: two dominant females, two non-dominant females and two males.
The figures, given in Table 11, clearly show a tendency for adults to assemble into subgroups led by one dominant female throughout the year.

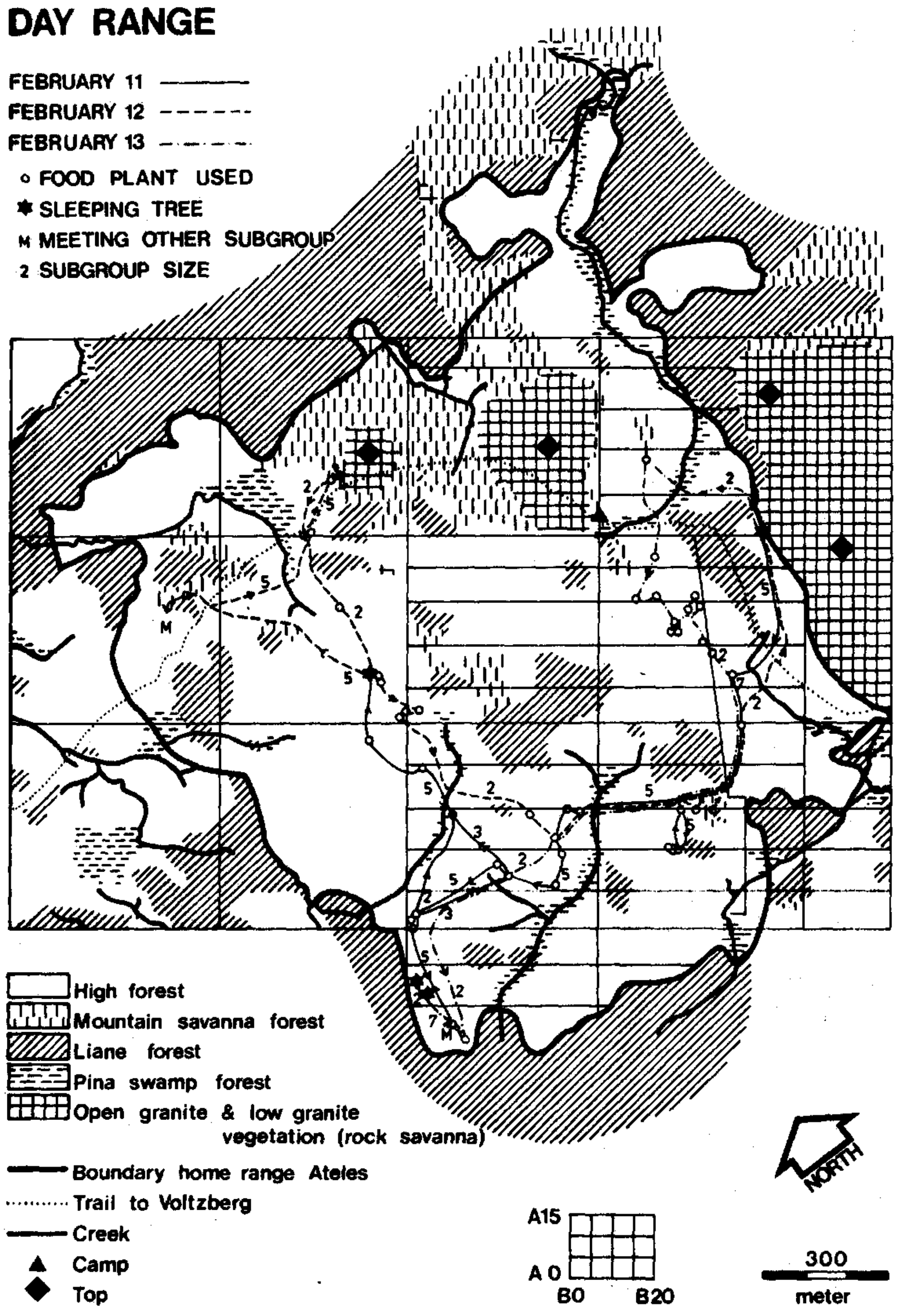


Fig. 28. Spider monkey subgroup sizes and routes on both February 11, 12 and 13, 1978, a certain dominant female (with juvenile) being the target followed, showing the pattern of temporary associations with this female leading the subgroup.

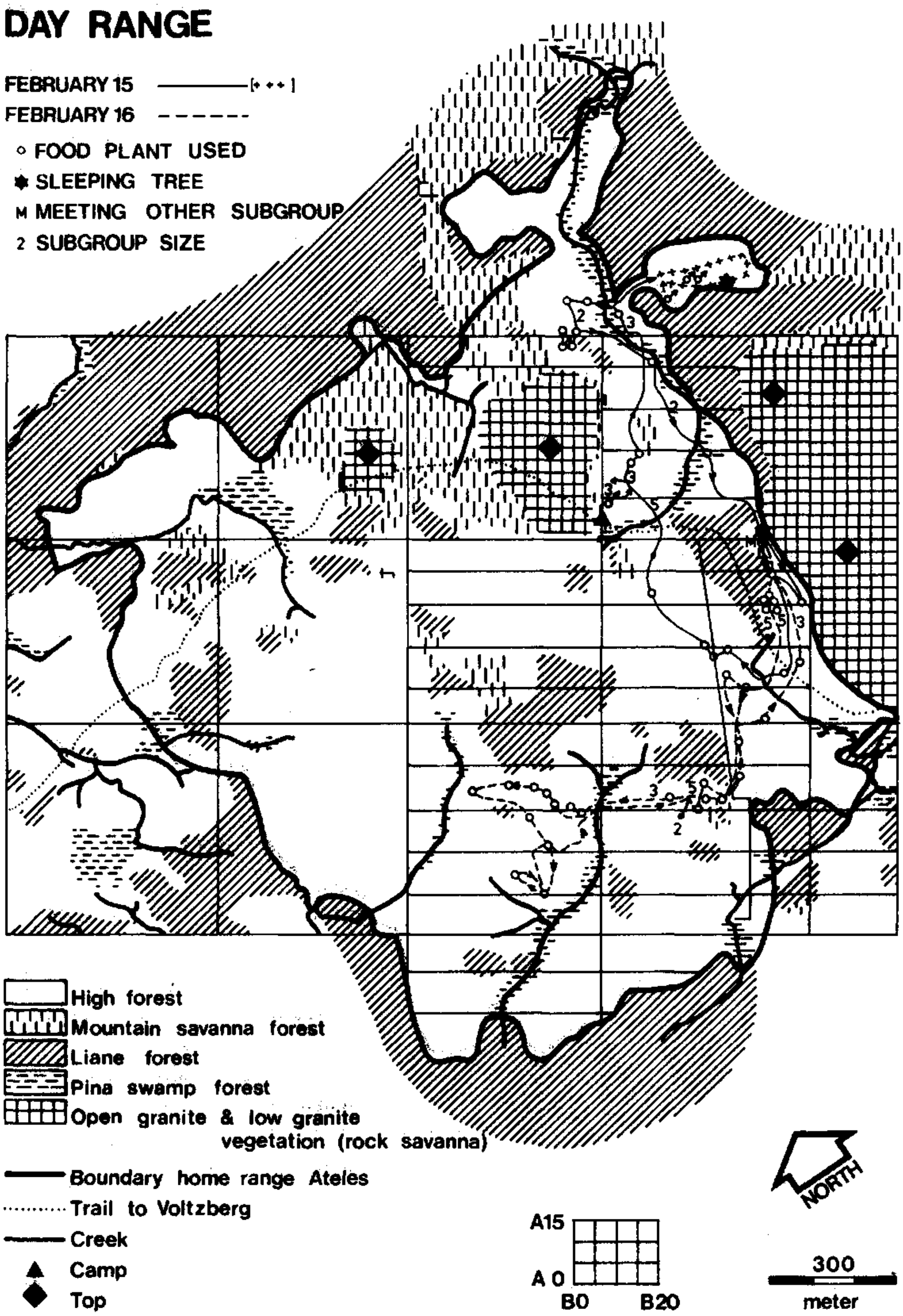


Fig. 29. Spider monkey subgroup sizes and routes on both February 15 and 16, 1978, a certain dominant female (with juvenile) being the target followed, showing the pattern of temporary associations with this female leading the subgroup.

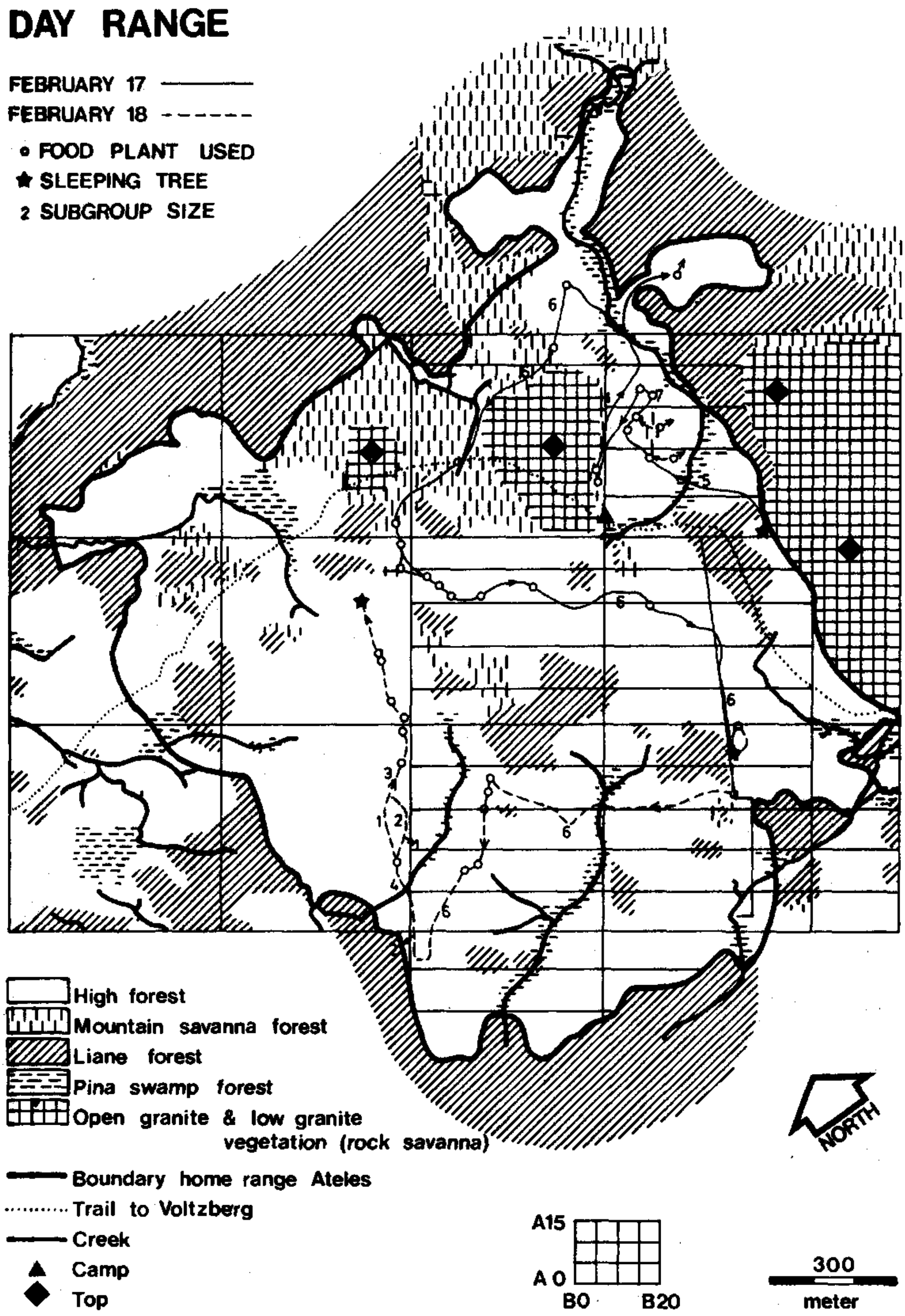


Fig. 30. Spider monkey subgroup sizes and routes on both February 17 and 18, 1978, a certain dominant female (with juvenile) being the target followed, showing the pattern of temporary associations with this female leading the subgroup.

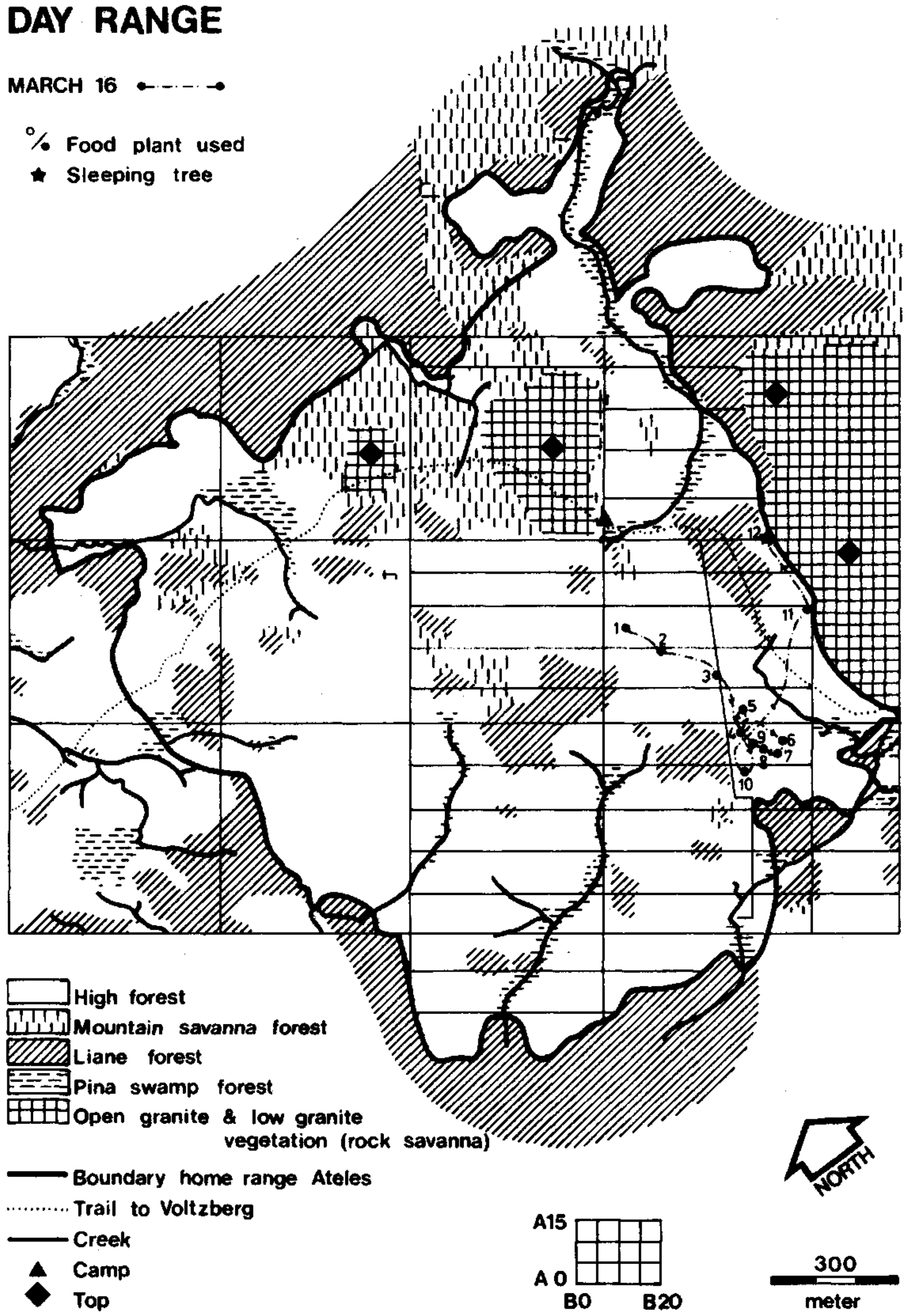


Fig. 31. Route followed by a non-dominant female on March 16, 1978, showing the incapability of pre-planning an economic route along food sources without double-backs and exploiting food sources more than once a day.

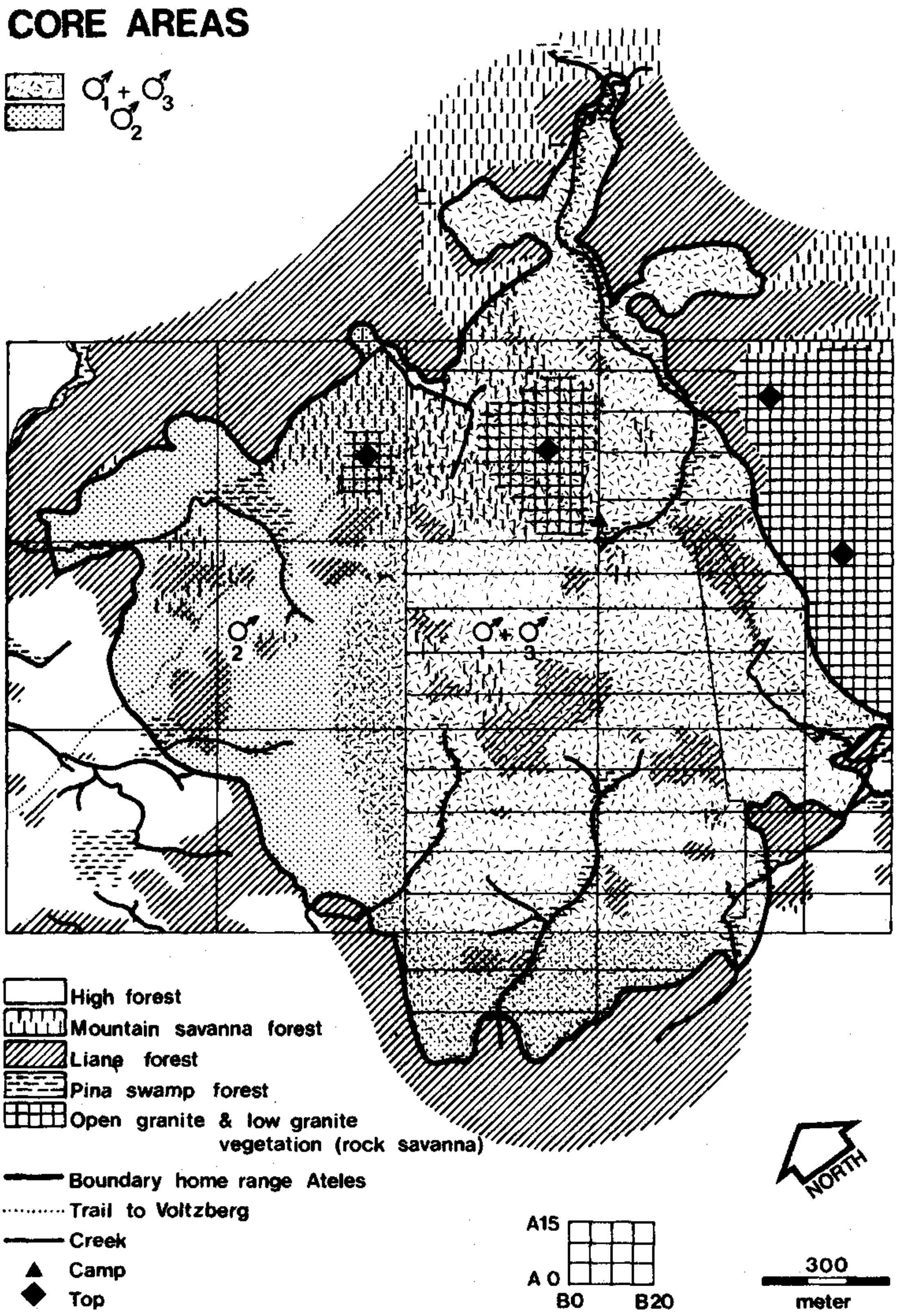


Fig. 32. Distribution of the male core areas within the spider-monkey group range. The ♂$_2$ core area corresponds about with the combined core area of the western set of dominant females, the ♂$_1$+♂$_2$ combined core area corresponds with that of the eastern set of dominant females. ♂$_3$ was found most frequently in the core-area overlap zones, where every group female could be encountered.

Considering subgroups consisting of at least one dominant female, the tendency to assemble into these subgroups is significant throughout the year, but lowest in July and August (39.0 and 40.5%, resp.), a period of distinct food shortage, and highest in April, May and June (between 94.1 and 96.6%), a period of food excess.

6.3.3. Subgroup size and subgroup composition. In Table 12, for the study group all subgroup sizes and compositions, observed during one year of intensive study, are listed and their frequencies are given expressed in terms of cumulated observation time (minutes) and percentage of total observation time (1061 hours). For this purpose, infants were considered unities with their mother, as long as they were not fully independently locomoting while travelling (from birth to about 12 - 16 months old). Subgroups of three or less individuals were observed slightly more frequently than subgroups of four or more individuals (53.3 and 46.7%, resp.). Most frequently a subgroup of three individuals has been observed (28.0%), followed by subgroups of two (19.1%) and four (18.6%) individuals. Solitary ranging animals were seen with a frequency of 6.2%, but they may be underestimated because of my preference to follow the larger subgroup in case one animal left the subgroup. Subgroups of 5, 6 and 7 animals made up for 12.7, 9.0 and 6.2% resp., whereas subgroups of more than 7 animals only made up for 0.24%.

Table 11. Intermonth variations in frequencies of four different subgroup categories composed of individuals ranging mainly within the B8-B20 area, the combined core area of one set of dominant females, selected because of being the best studied part of the group. Six adults are involved: two dominant females (♀), two non-dominant females (♀), and two males (♂$_1$ and ♂$_3$). For the sake of determining association patterns between and with dominant females, juveniles were considered unities with their mother (both dominant females)

Month	Subgroups containing				Total observation time in minutes
	No ♀	One ♀	Two ♀♀	At least one ♀	
January	23.7	57.7	18.7	76.3	7775
February	27.1	39.6	33.3	72.9	9562
March	17.4	51.7	30.9	82.6	8565
April	3.4	57.9	38.7	96.6	4690
May	2.2	67.5	30.3	97.8	3000
June	5.9	90.8	3.3	94.1	3804
July	61.0	39.0	0.0	39.0	2218
August	59.5	40.5	0.0	40.5	2288
September	22.9	72.5	4.6	77.1	2260
October	19.7	62.0	18.3	80.3	8018
November	23.9	41.8	34.3	76.1	11244
December	9.1	72.5	18.4	90.9	6750

The most frequently observed subgroup composition was the combination ♂ - ♀+juv (18.5%), followed by that of ♂ - ♀ - ♀+juv (12.3%). The subgroup compositions ♀+juv (8.9%) and ♀ - ♀+juv (8.6%) were common. Solitary ranging males were observed with the same frequency as solitary ranging females with or without an infant (3.1%), but as stated before, these frequencies can be regarded to be underestimated.

Table 12. Mean size frequencies of independent, completely aged and sexed subgroups during a full year of observation, and the nights spent together for each subgroup category. For this purpose, infants were considered unities with their mother, as long as they were not fully independently locomoting while travelling.
i = infant, j = juvenile, s = subadult

Subgroup		Cumulated observation time in minutes		Total nights		% Total observation time	
Size	Composition						
1	♂	1959	3962	8	13	3.1	6.2
1	♀±i	2003		5		3.1	
2	♂,♀	3869	12134	6	19	6.1	19.1
2	♀+j	5649		9		8.9	
2	2♂♂	2492		3		3.9	
2	2♀♀	124		1		0.2	
3	♂,♀+j	11753	17798	23	36	18.5	28.0
3	♀,♀+j	5445		11		8.6	
3	2♂♂,♀±i	25		-		0.04	
3	♂,2♀♀±i	485		1		0.8	
3	♀,♀±i,s♀	90		1		0.1	
4	2♂♂,♀+j	3396	11816	5	27	5.3	18.6
4	♂,♀,♀+j	7836		19		12.3	
4	2♀♀,♀+j	350		1		0.6	
4	♀+j,♀+j	234		2		0.4	
5	♂,♀+j,♀+j	4206	8077	12	20	6.6	12.7
5	♀±i,♀+j,♀+j	2654		4		4.2	
5	2♂♂,♀,♀+j	1128		2		1.8	
5	♂,♀,♀±i,♀+j	89		-		0.1	
6	2♂♂,♀+j,♀+j	1497	5742	-	11	2.4	9.0
6	♂,♀±i,♀+j,♀+j	3888		10		6.1	
6	♂,♀,♀±i,s♀,♀+j	252		1		0.4	
6	2♂♂,2♀♀,♀+j	105		-		0.1	
7	2♂♂,♀,♀+j,♀+j	3687	3927	1	2	5.8	6.2
7	♂,♀,♀±i,♀+j,♀+j	240		1		0.4	
8	2♂♂,2♀♀,♀+j,♀+j	15	15	-	-	0.02	0.02
9	3♂♂,2♀♀,♀+j,♀+j	158	173	-	-	0.2	0.2
9	2♂♂,♀,♀+j,♀+j,♀+j	15		-		0.02	
		+ 63644			+ 138		+ 100.0

The combination ♂ - non-dominant ♀ was observed with a frequency of 6.1% and mainly concerned a receptive female. A subgroup consisting of at least one male and other animals was observed with a frequency of 70.9%. A subgroup of only two males made up for 3.9%, whereas a subgroup of only three males never has been seen during the present study. Subgroups with at least two males among others were observed with a frequency of 15.7%,whereas a large subgroup including all three males was observed in only 0.2% of the total observation time.

6.3.4. Seasonal variation in grouping behaviour. Because spider monkeys are specialized frugivores, feeding predominantly on mature fruits, not produced in large amounts simultaneously by a particular food plant, subgroup size has to be restricted to avoid strong agonistic behaviour in that food plant. Theoretically, subgroup size will be positively correlated with food patch size.

In Table 13, all subgroup size classes observed and the percentage of total observation time for each size class are given for each month of the year. To make the figures easier to interprete, in Table 14 the subgroup size classes have been reduced to two: subgroups of more than 3 and subgroups of 3 or less fully independently locomoting individuals. Subgroups were smallest during the first part of the long dry season, a period of food scarcity (especially of mature fruits), with significant minima in July, August and September (26.8, 18.4 and 4.6%, resp., for subgroups of more than 3 individuals). On the contrary, subgroups were largest during the peak of the long wet season, when apparently an excess of mature fruits existed, with April and May as significant maxima (77.2 and 65.4%, resp., for subgroups of more than 3 individuals). During the rest of the year figures are relatively constant, and subgroups of more than 3 individuals range from about 35 to 45%.

Table 13. Intermonth frequency variations in size of independent subgroups expressed as the percentage of total observation time for size classes of 1 - 9 individuals in each month of the year. The relatively low observation time totals in the months July, August and September are due to the low energy budget, the relative silence and the smaller subgroup sizes of the monkeys in this period of food scarcity, making it much harder to come in contact with them

Month	Number of individuals per subgroup									Total obs. time in minutes
	1	2	3	4	5	6	7	8	9	
January	19.4	8.8	36.9	15.2	4.2	14.5	0.9	-	-	7869
February	4.7	43.2	14.6	4.2	22.5	7.7	3.1	-	-	9584
March	17.1	3.0	37.8	11.0	7.9	13.0	10.0	-	0.2	8578
April	3.4	0.1	19.3	38.5	8.8	15.1	14.8	-	-	4690
May	1.0	21.4	12.2	46.2	8.2	3.5	7.5	-	-	3000
June	5.2	29.5	19.8	41.6	3.1	0.8	-	-	-	3834
July	2.9	45.7	24.6	26.8	-	-	-	-	-	2218
August	10.5	24.1	47.0	18.4	-	-	-	-	-	2288
September	0.0	45.9	49.5	-	4.6	-	-	-	-	2260
October	7.6	5.5	45.5	13.1	15.5	3.6	9.2	-	-	8053
November	7.3	21.9	24.6	10.2	15.9	9.6	9.0	0.1	1.4	11619
December	7.4	3.8	44.6	23.6	13.9	6.7	-	-	-	7002

A subgroup of four or more independently locomoting animals, following an itinerary determined by a dominant female, usually did not feed with more than three animals at the same time on one particular food source, except when a sleeping tree also provided ample food or when a large-crowned flowering or flushing tree offered enough space to feed at ease together. While at least the dominant female with her offspring was feeding on a particular food plant, some others (especially non-dominant females) were searching for or feeding on nearby food sources, sometimes of inferior quality, and often entered the food plant choosen by the dominant female when the other animals were resting or travelling to the next food source. In this way, the itineraries are the same for all subgroup participiants, while the activity patterns are quite simultaneous. Also, non-dominant females and males can learn about important food sources available and their location, a knowledge needed for the times they will be ranging solitary or associated with one or more non-dominant female(s) and/or male(s). This foraging pattern clearly can be followed only when food supply is high and fruiting food plants occur in relatively high densities, making likely the locating of another food source nearby. During the present study, this condition was fulfilled particularly in April and May, when trees of *Guarea grandifolia*, *Tetragastris altissima*, *Tetragastris panamensis*, *Protium polybotryum* and *Protium neglectum* were fruiting abundantly, species with overall densities of resp. 214, 777, 133, 103 and 148 full-grown trees per km^2 and locally even reaching much higher densities (Table 1; Appendix).

Table 14. Intermonth frequency variations in two size classes (≤ 3 and > 3 individuals) of independent subgroups expressed as the percentage of total observation time and the percentage of the total number of observed nightly subgroup sizes in the same size classes in each month of the year

Month	% Total observation time per subgroup size class		Total obs. time in minutes	% Total night observations per subgroup size class	
	≤ 3 ind.	>3 ind.		≤ 3 ind.	>3 ind.
January	65.1	34.9	7869	62.5	37.5
February	62.5	37.5	9584	60.0	40.0
March	57.9	42.1	8578	50.0	50.0
April	22.8	77.2	4690	25.0	75.0
May	34.6	65.4	3000	20.0	80.0
June	54.5	45.5	3834	37.5	62.5
July	73.2	26.8	2218	100.0	0.0
August	81.6	18.4	2288	100.0	0.0
September	95.4	4.6	2260	100.0	0.0
October	58.6	41.4	8053	60.0	40.0
November	53.8	46.2	11619	60.8	39.2
December	55.8	44.2	7002	77.0	23.0

What do dominant females do in times of food scarcity? Of a total of four dominant females in the study group, two were best studied, throughout the year mainly using the area between the parallels on B8 and B20, whereas the other two mainly used the area between the parallels on B1 and B10, within the perimeter of the home range (Fig. 32). In addition to the strip between B8 and B10, an important area of overlap between the core areas of both sets of dominant females could be found to the south of the B-axis, between B10 and B18. In this area every member of the group could be encountered regularly. The non-overlapping areas were not exclusively used by one set of dominant females with their associates, but seemed to be best known by the respective set of females. The best studied set of dominant females, using in particular the first area, more frequently visited the second area than reversely the other set the first area (between the parallels on B10 and B20, and to the north of A15). This occurred especially during October and November, when still preferred food (nutritive fruits) was scarce and the eastern subgroups were foraging regularly on infructescences of *Philodendron* spp., fruits of *Ecclinusa guianensis* and flush leaves of *Ceiba pentandra*, foods which in particular or more often could be found in the second area.

The dominant females of each set usually exploited different but partly overlapping core areas within their general range. The core-area overlap appeared to grow with increasing food supply. In times of food scarcity (esp. in July, August and September), one dominant female of the eastern set almost exclusively exploited a core area situated between the B8 and B15 trails, and especially to the south of the B-axis, while the other dominant female almost exclusively used a core area between the B15 and B20 trails, and in particular to the north of the A15 trail. Each core area covered about 100 ha. In times of food excess, this set of dominant females used almost the whole area of both core areas combined, so about 200 ha. The western set of dominant females exploited a combined area of about 120 ha.

Looking at subgroups containing both dominant females of the eastern set and one or more of the other four adults ranging mainly within this area, the following frequencies were observed: 18.7% (January), 33.3% (February), 30.9% (March), 38.7% (April), 30.3% (May), 3.3% (June), 0.0% (July), 0.0% (August), 4.6% (September), 18.3% (October), 34.3% (November) and 18.4% (December) (Table 11).

During the first part of the long dry season (July, August and September), a period of distinct food scarcity, both dominant females almost never joined in one subgroup, whereas in November, at the end of the dry season, a peak of joining can be seen. One reason for this pattern may be the abundance of large-crowned flushing and flowering food plants in November, offering at the same time enough food and space for relatively large subgroups (Table 14; 46.2%, for subgroup sizes >3), like *Ceiba pentandra* (flush leaves and flowers), *Vataireopsis speciosa* (flush leaves) and several *Bignoniaceae* (flowers). A second reason may be the already mentioned regular visits of both dominant females, often joining in one subgroup, to the core areas of the western set. About as high frequencies of joining are reached in the period February - June, when the supply of mature fruits is highest and several important food species fruit abundantly. The second peak of joining can be seen in April, when a food excess appeared to exist. The food supply in October, December and January was fairly good, resulting in medium-sized frequencies of about 18%.

What mechanism governs the decrease of mean subgroup size in times of food shortage, just when it would be most advantageous for males and non-dominant females to learn about food sources from dominant females by conspecific cuing?

Both dominant females of a set clearly preferred regular contact with one another by merging subgroups, when food supply allowed foraging in relatively large subgroups. This may have a social reason. The offspring of these females appeared to enjoy very much one another's company and, when in the same subgroup, much time was spent playing together.

That exchange of knowledge on available food sources is not vital for females may be demonstrated by the way both females of a set acted when belonging to the same subgroup. In these cases, they alternately determined subgroup activity patterns, and frequently separated in two subparties for a short time, each leading part of the subgroup along slightly different itineraries before merging again. For the sake of foraging success, dominant females obviously do not need one another. Therefore, no agonistic behaviour has to force them into exploiting different core areas, when food shortage is present or soon to be expected. This pattern is caused by the food shortage itself.

In this view, it may be interesting to note that already in June both dominant females of the B8-B20 set rarely assembled into one subgroup (3.3%) (Table 11), whereas food supply was still fairly good (Table 1; Fig. 9). The pattern may be explained by the following. For optimal exploiting different core areas in July, dominant females may have to start in time with checking food sources for the near future, since the ecological change appeared to occur quite abruptly in the course of July. It may need some time to learn about and memorize all food sources soon becoming available in a smaller but less known area.

The above argued mechanism of dominant female-core area-splitting alone, will drastically decrease mean subgroup size during the period of food shortage. Males and non-dominant females alternately or more specifically may join dominant-female subgroups or form small subgroups with one another. Calculating the monthly figures for each category of subgroup composition, it appeared that subgroups of one or more individuals, not containing a dominant female, gave much higher frequencies in July and August (61.0 and 59.5%, resp.), than in the rest of the year (ranging from 2.2 to 27.1%), thus especially in months of distinct food shortage (Table 11). Whether this association pattern of males and non-dominant females results after increased agonistic behaviour from the side of dominant females is not fully clear. Overt aggression regularly has been observed of males towards non-dominant females and juveniles, especially when feeding at the same time on a particular food source. Some overt aggression was observed of a dominant female towards the younger male within the group, which took place mainly in July. Aggressive behaviour of a dominant female directed towards a non-dominant female has been observed very rarely, but when occurring, could be severe. Moreover, a comparable type of appeasement behaviour as performed mutually by males, when meeting one another after some time, occasionally was observed in females, initiated by the non-dominant female meeting a dominant female, and was attended with pectoral sniffing and embracing.

6.3.5. Male strategy. The study group counted three adult males, a very old one (♂$_1$), one of middle age (♂$_2$) and a young male of about 6 years old (♂$_3$).

When male spider monkeys, belonging to the same group, meet one another after some time, they may perform a kind of greeting ceremony, mutually embracing and pectoral sniffing each other's scrotum. By analysing greeting behaviour among males, it appears that it is initiated by the lower-ranking male, and it may be regarded as appeasement behaviour. The old male (♂$_1$) appeared to be highest in rank, followed by ♂$_2$, ♂$_3$ and a juvenile-3, resp.

Adult males never have been observed outside the perimeter of the group's range, and mostly, but not exclusively, ranged within certain core areas. The older males (♂$_1$ and ♂$_2$) each used about the same area as the combined core areas of each set of dominant females, the eastern and western set, resp. The young male, ♂$_3$, alternately used one of the two male core areas, but more often could be seen within the eastern area, and especially within the overlap zones (both to the south of the B-axis and between the B8 and B10 trails) (Fig. 32).

Each male appeared to prefer joining a subgroup of one or more group members (70.9% of the total observation time), especially when it contained one or more dominant females (60.0%). The males usually associated alternately with each female of a set, or more specifically with a certain dominant female. For instance, ♂$_1$ was observed most frequently in a subgroup led by the mother of the male juvenile-3, whereas ♂$_3$ alternately joined a subgroup led by a dominant female of the eastern set or, less often, of the western set.

Both males, ♂$_1$ and ♂$_3$, were seen visiting the ♂$_2$-core area more often than the reverse, such visits taking place especially in the second part of the long dry season. In this period, the three males came repeatedly together with other group members in a particular emergent tree of the species Hymenaea courbaril (Fig. 33, no. 38), obviously functioning as a sort of social meeting place. At these occasions the largest subgroups could be counted, ranging from 7 to 9 independently locomoting individuals, resting in the huge crown for hours, while the juveniles were playing with each other and/or an adult. Otherwise, the three adult males of the study group were observed together only during the very rare territorial boundary conflicts with members of group II, to the south. In these conflicts, one male started long calls and in cooperation with one or more females performed siamang-like barking duets, what caused an invasion of neighbouring subgroups, while the members of the other group responded with similar behaviour at the other side of the boundary. The males of both groups probably were in sight of one another at a distance of 100 - 200 m, acting very upset and performing an aggressive display for a considerable time. Especially the males within the subgroup shook branches and broke off twigs, branches and even dead boughs, uttering long calls ('whoops') and barking in cooperation with one or more females ('ook-barking') (Klein, 1972). Several times, the males were observed performing reassurance behaviour by mutually embracing and pectoral sniffing or only by shortly touching with the hand each other's back, shoulder or arm. These territorial conflicts, initiated by a male, were very rare and in the course of the present field study only a few times such spectacles were heard among other groups in the Raleighvallen-Voltzberg Reserve. Perhaps the rariness of territorial conflicts with the study group may be explained by the relatively few boundary lines with other groups, caused by the geographical barriers like liane forest and open granite forming for a great part the limits of the group's range.

6.3.6. Calling behaviour. Only male spider monkeys are able to perform long calls or 'whoops'. On the forest floor, these long calls are audible at a distance of 800 - 1000 m. High up in emergent trees, long calls can be heard over about 2000 m, whereas from the top of the Voltzberg (240 m) one even could locate calling males over 3000 - 4000 m. Assuming that spider monkey sense of hearing is at least as good as human one, in an emergent crown spider monkeys will be able to catch every intragroup long call, since the largest imaginable distance between two points within the perimeter of the home range amounts to 2400 m (Fig. 32).

Long calls of the different males in the study group could easily be recognized individually by the sound frequencies, and both the amount and length of intervals between notes.

At least five types of male long call could be distinguished, superficially sounding similar but performed in different behavioral context:

1) Morning Long Calls - (MLC)	Usually performed once or only few times during the period of increase in foraging activity (e.g., between 6.00 - 7.30 h), and as a rule answered by one or more males of the same network. It seemed meant to inform males of one another's location and direction of travel. Also, estrous females could be attracted in this way.
2) Evening Long Calls - (ELC)	Usually performed only once, just before or after a male entered a sleeping tree. It seemed meant to inform all group members of the location of the sleeping site selected for the night. Nearby parties, thus, could be attracted to assemble into larger units. When more males were involved, usually only one of them gave the long call. Mostly, an ELC was not answered immediately by

one or more other males. The males seemed to perform ELC's at different times, since they usually did not simultaneously settle for the night. Also, it must be stated that by no means ELC's were given every day. When it was raining, the males kept silent. On the other hand, especially during the long dry season ELC's were rare.

3) *Food Long Calls* - (FLC)
These long calls could be given all day, in particular just before or while feeding on an important, usually primary food source, probably well-known to most or all group members. In most cases, FLC's were not answered, and seemed to be used for spacing purposes. In these cases, the male often was part of a relatively large subgroup and usually no merging of subgroups took place some time after. FLC's seemed meant to tell others that a nearby food source was being depleted at that moment, and therefore might better be dropped out of a dominant-female's foraging route.

4) *Contact Long Calls* - (CLC)
These long calls could be given by a male just after loosing contact or leaving a subgroup, apparently in an attempt to influence the direction of travel choosen by the dominant female of that subgroup. In this way, it could happen that the male attracted the subgroup and joined it again, but often he seemed not to succeed. This behaviour could be observed for instance, when a male left the subgroup in order to contact another one nearby, but after meeting it decided not to join. Or, when the subgroup led by a dominant female took one out of two routes, ecologically determined beforehand for the rest of the day (relating to granite outcroppings, narrow paths of high forest in between liane forest, etc.). In that case, the male could stay for a while at the junction of both routes, giving CLC's repeatedly.

5) *Alarm Long Calls* - (ALC)
These long calls could be given all day by males, but especially when being upset by the localization of a large carnivore (e.g., jaguar) or an unfamiliar human intruder, by alarmed terrestrial animals on flight (e.g., tinamous, quails, trumpeters, curassows, agoutis, deer, peccaries), or combinations of it. Also, they could be performed during long-distance agonistic behaviour against one or more adult males of a neighbouring network. ALC's were combined with 'ook-barking', usually in cooperation with one or more adults, and sometimes lasted over one hour. Afterwards, most adults appeared to stay very unstable for a while and the slightest incident could reinitiate the behaviour. For instance, although the observer did not play a part in starting the aggressive display, later on it could be directed on him simply by his stepping on a dead branch. ALC's seemed meant to attract nearby parties for assembling in an aggressive display, and were never answered by calls of other parties belonging to the same network.

During the first part of the long dry season, long calls were heard only occasionally. Spacing may be optimal when males are relatively silent, especially considering the small day ranges and the drastically decreased energy budget in this period of food shortage. Like for the observer, it will be much harder for individual spider monkeys to encounter subgroups if they like to. The aggregating component of male long calling behaviour has been omitted, while the spacing component seems to be more important during more favorable times, when day ranges are much larger and energy budget is increased considerably. Moreover, during the dry season the available food sources are, in general, quite different from those offered during the rest of the year, making quick depletion unlikely. Ripe fruits of Apeiba spp. and Dimorphandra multiflora are important food sources, which are present over long periods, while foods like flush leaves and flowers usually are widely dispersed and available in large quantities for a short time.
During July and August, especially males and non-dominant females could be seen staying all day or longer within a small area, that offered a few of these food sources, while resting most of the time. The decreased energy budget may be explained not only by the decline of overall food supply but also by the dietary shift, with flush leaves and flowers constituting a considerable part of the diet. The proportion of day-time spent on feeding and moving is negatively correlated to the proportion of foliage in the diet (Clutton-Brock, 1977).

6.3.7. Sleeping trees. The tendency to aggregate in sleeping trees is illustrated in Table 14. The percentage of total nights spent together is given for two subgroup size classes, with three or less, and more than three independently locomoting individuals. Comparing these percentages with day-time figures, a strong tendency to aggregate in sleeping trees can be noted in May and June, while a strong tendency for spacing is demonstrated in July,August and December.

A spider monkey group does use a lot of sleeping trees during a whole year, but only a few are important all year round. This may be explained by the sleeping tree its permanently open crown (e.g., in Hymenolobium spp., Parkia pendula and Vochysia tomentosa). Also, its strategic location within the perimeter of the home range or core area may play a role and/or the relatively high food supply to be found in the direct environment during most of the year.
In total, 43 different sleeping trees were used by members of the study group (Fig. 33). Counting the number of sleeping trees per species gave the following order: Buchenavia capitata (10), Vataireopsis speciosa (5), Couratari stellata (4), Hymenolobium petraeum (4), Hymenolobium flavum (4), and Parkia pendula (3).
Ranked according to the number of nights spent in a particular sleeping tree, the following were most important: Hymenolobium flavum (31), Vochysia tomentosa (16), Newtonia suaveolens (12) and Vataireopsis speciosa (8) (Fig. 33, no. 1,6,12 and 16, resp.).
The following criteria seem to be used by spider monkeys in selecting a sleeping tree:
1) The tree must be an emergent, not only determined as such by its absolute height, but also by its relationship with the environment. The crown must be fully free from the canopy beneath. Usually, it will be entered by swinging or leaping across a gap from the periphery of an adjacent crown or by ascending the huge trunk using stems of lianes and epiphytes and/or aerial roots. In particular, emergents at edges of natural clearings, granite outcroppings, low forest or liane forest are preferred.
2) A broad, open crown is preferred when it bears small leaves, stands leafless or is in early flush.
3) The crown must be structured with more or less horizontal branching. Spider monkeys prefer almost horizontally forked branches for long-rest-

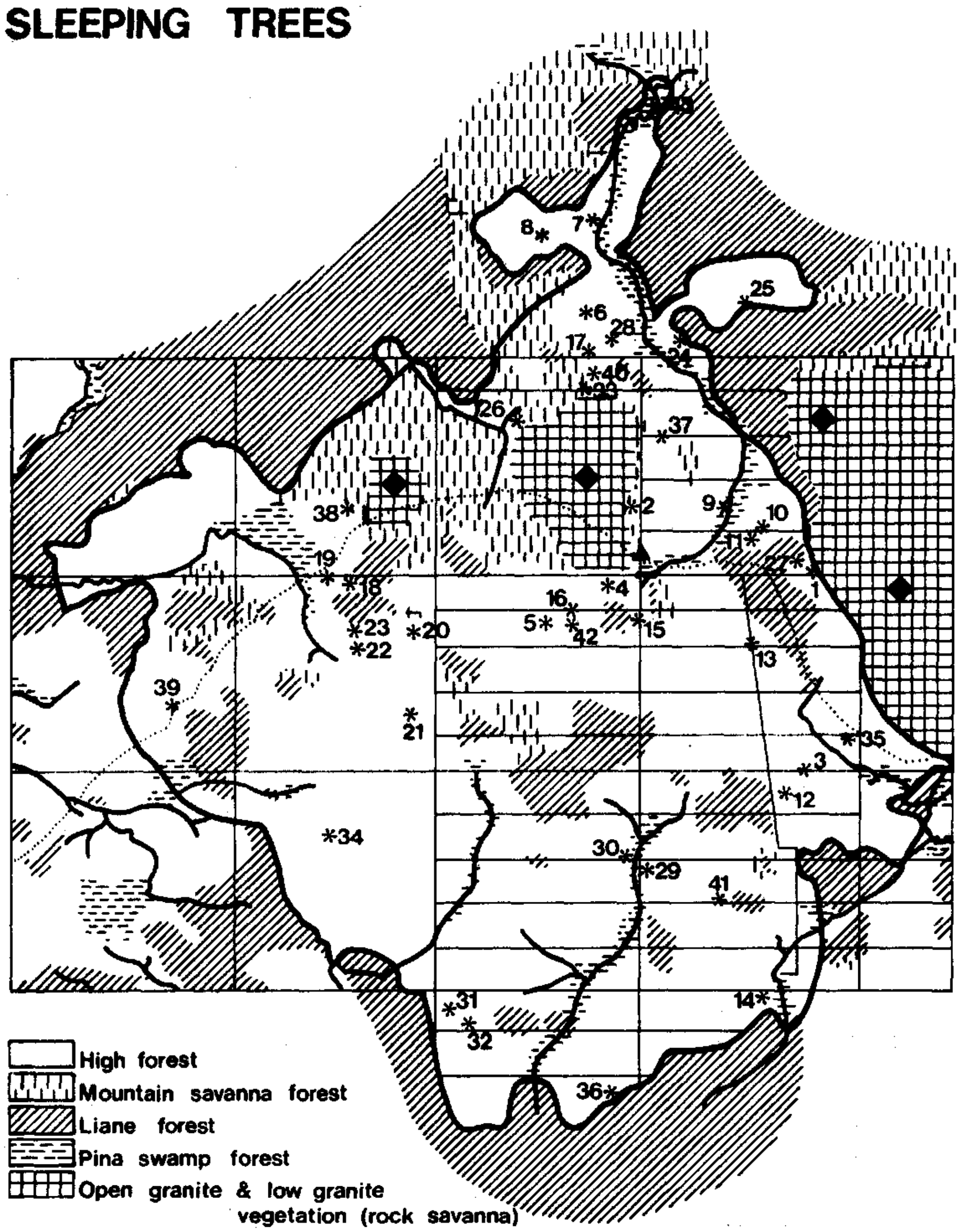


Fig. 33. Location and species of sleeping trees used by members of the spider monkey group in the Voltzberg study area: 1. Hymenolobium flavum - 2. Hymenolobium petraeum - 3. Enterolobium schomburgkii - 4. Couratari stellata - 5. Buchenavia capitata - 6. Vochysia tomentosa - 7. Buchenavia capitata - 8. Parkia pendula - 9. Dimorphandra multiflora - 10. Buchenavia capitata - 11. Cedrelinga cateniformis - 12. Newtonia suaveolens - 13. Hymenolobium petraeum - 14. Parkia pendula - 15. Buchenavia capitata - 16. Vataireopsis speciosa - 17. Hymenolobium flavum - 18. Ceiba pentandra - 19. Parkia nitida - 20. Buchenavia capitata - 21. Buchenavia capitata - 22. Buchenavia capitata - 23. Buchenavia capitata - 24. Couratari stellata 25. Parkia pendula - 26. Couratari guianensis - 27. Vataireopsis speciosa 28. Vataireopsis speciosa - 29. Couratari stellata - 30. Vochysia tomentosa 31. Vataireopsis speciosa - 32. Vataireopsis speciosa - 33. Hymenaea courbaril - 34. Hymenolobium petraeum - 35. Hymenolobium petraeum - 36. Hymenolobium flavum - 37. Hymenolobium flavum - 38. Hymenaea courbaril - 39. Buchenavia capitata - 40. Dimorphandra multiflora - 41. Buchenavia capitata 42. Couratari stellata - 43. Qualea dinizii.

ing postures, usually sleeping in a reclining posture full length or in a more or less asymmetrical sitting posture.
4) The tree must be located strategically regarding the foraging grounds for the late afternoon and next day's morning. Spider monkeys seem to be very hungry after awakening and to prefer having one or more interesting food sources near the sleeping tree, providing a good breakfast at the start of a day's itinerary.
5) A particular sleeping tree may be given priority, when providing food at the spot. This may be fruits, flowers or flush leaves, or edible epiphytes and/or lianes growing in its crown. When providing edible flowers or flush leaves, the monkeys prefer to consume these during the late afternoon, before choosing their sleeping site for the night.

The only valuable explanation for the strong selectivity in the choice of sleeping trees fulfilling the three first mentioned criteria will be predation at night. Spider monkeys reacted very upset with thrilling sqeaks when they were encountered in a sleeping tree at full dark, being unable to identify the intruder at the forest floor. Occasionally, these specific vocalizations were heard at night in the camp, probably as reaction on disturbance by a terrestrial carnivore or herbivore near a sleeping tree.

Except for infants, all subgroup members are scattered over a sleeping-tree crown always on branches, but with preference for the center and the upper part. Individual monkeys appeared to possess a personal sleeping site, at least in frequently used sleeping trees. By using slender perches in open, isolated crowns the monkeys may be readily awakened by a possible felid climbing the tree.

During the present field study, no predation of spider monkeys has been observed. Only a young infant died for an unknown reason.
Day-time predation probably is non-existent in spider monkey community. Several times, spider monkeys were seen feeding in the periphery of open crowns, while a harpy eagle (Harpia harpyja) was flying around, but in no way they were upset by its presence. Juveniles kept on feeding at vulnerable sites, and only once a short branch shaking display was performed to scare off this large raptor.
Juvenile spider monkeys were observed curiously following tayras (Eira barbata) at short distance for a while. Many hairballs, regurgitated by the jaguar (Panthera onca) living in the area, and dung samples were analysed and appeared to contain only nails, hairs and bones of terrestrial animals. Ocelots (Felis pardalis) were living in the area, and once an ocelot was observed fighting with two tayras on the forest floor, while a male spider monkey descended to about 10 m above the fighting animals and barked at them.

Spider monkeys are very defensible animals, apparently not afraid for any day-time intruder, including man (unless experience with guns has taken place). At first contact with human intruders, spider monkeys usually perform a branch-shaking and branch-breaking aggressive display directed towards the intruder. Apart from this, the males may give long calls or perform 'ook-barking' in cooperation with one or more females. Other subgroups may join the aggressive display. Dead branches or even boughs are selected, preferentially those right above the intruder, and broken off. This display may be performed too, when detecting a large felid walking on the forest floor. In this context, it may be interesting to emphasize that spider monkeys appeared to become upset especially by alarmed terrestrial animals on flight, like tinamous, quails, trumpeters, curassows, agoutis, deer, peccaries and tapirs.

6.4. Reproductive Biology and Sexual Behaviour

According to Eisenberg (1976), spider monkey females giving birth to an infant will pass into a lactation anestrus for a period of 15.3 to 24 months. The data gathered in the Voltzberg study area, however, indicate a lactation anestrus for a period of about three years. An infant, born about October 1974, has been regularly nursed until September 19, 1977. A month later, its mother came in estrus for the first time. Another dominant female gave birth to an infant about January 1975, and nursed it until about December 1977. This female came in estrus for the first time on January 22, 1978. Several other females of *Ateles paniscus* in Surinam were observed nursing a juvenile-2 or even a juvenile-3. Old juveniles were nursed only few times a day (mean duration was two minutes), in particular while resting in a sleeping tree before nightfall. It appeared that these few nursing bouts were sufficient for the mother to remain in anestrus. The difference between the Eisenberg data and the data collected on feral spider monkeys in Surinam may be explained by the fact that, in captivity, the period until social weaning for young spider monkeys is much shorter.

Female spider monkeys, coming into estrus, show a tendency to manipulate, inspect and rub the clitoris. The duration of sexual receptivity in Surinam spider monkeys ranged from 8 to 10 days. The interestrus interval lasted in average 15 to 17 days. This agrees with the cyclical uterine bleeding of adult females described by Goodman and Wislocki (1935), which occurred every 26 to 27 days.

In captive spider monkeys, gestation has been calculated at 226 to 232 days. The interbirth interval is a function of the duration of lactation and the number of estrus periods needed for successful conceiving. Interbirth intervals in captive *Ateles fusciceps* ranged from 22.8 to 31.5 months (Eisenberg, 1976). The range for *Ateles geoffroyi* would be 17 to 45 months (Dare, 1974) or 22 to 45 months (Eisenberg, 1976). Interbirth interval in feral *Ateles paniscus* in Surinam appeared to be about four years (ranging from 46 to 50 months). These comparisons only include cases where the mother reared her young to social weaning.

One of the dominant females was observed copulating 11 times, spread over 8 successive estrus periods. Another dominant female was observed copulating 7 times spread over 3 estrus periods. Successive estrus periods of five females belonging to the study group are given in Fig. 34. Unfortunately, at the end of the field period, the two best studied females did not become pregnant yet. Another female was lost out of sight after 5 successive estrus periods. The fifth female belonged to the western set of dominant females, and copulated with ♂$_1$ and ♂$_3$ once, but regular contact was not kept later on.

In Surinam, *Ateles paniscus* appeared to show a birth peak in the period November - February, at the end of the long dry season and during the short wet season. None of six females shot by hunters in Lely Mountains in the period February - April, 1976 contained a fetus (Mittermeier, 1977). Klein (1971) suggests that neither captive *Ateles geoffroyi*, nor feral *Ateles belzebuth* in Colombia exhibit a birth season. In contrast, Eisenberg (1976) indicates, that *Ateles fusciceps* in captivity shows a tendency towards two birth peaks and suggests estrus synchrony. Fig. 34 shows estrus synchrony in four of five female *Ateles paniscus* in Surinam in the period October, 15 to at least April. The female, giving birth to an infant on April 17, 1978, lost her previous infant in 1977, a fact that perhaps may explain asynchrony in estrus compared with the other females.

An estrus season from the end of the long dry season onto halfway the long wet season may agree with the seasonal variations in food patch size and grouping behaviour as described before. During the period of

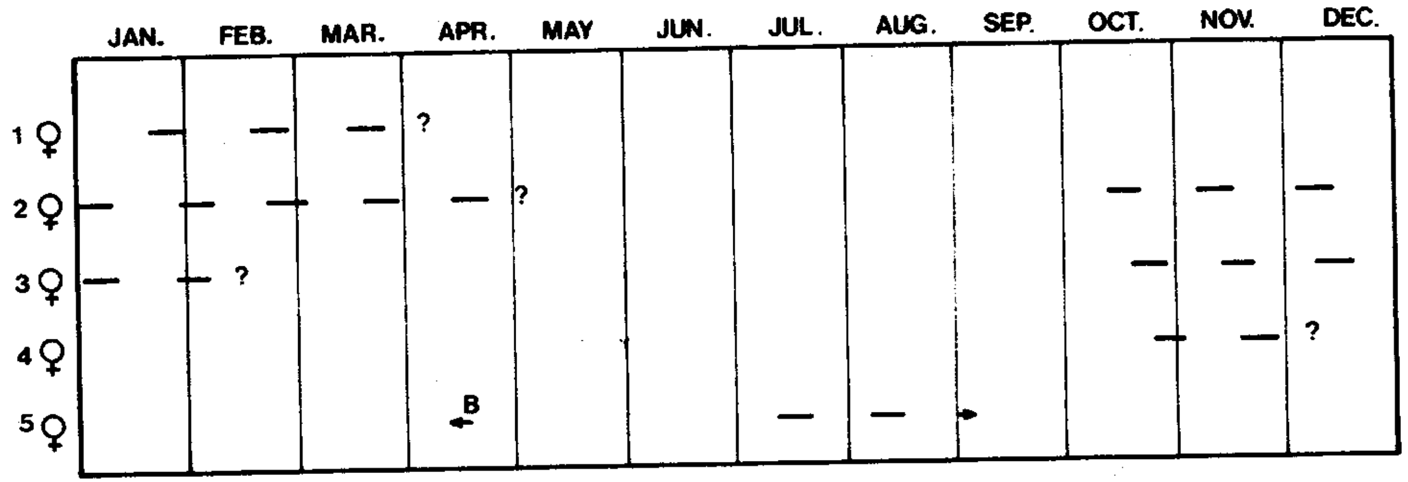


Fig. 34. Estrus periods in five adult females, belonging to the spider monkey study group, as observed from May 1977 to May 1978.
The females 1, 2 and 4 are dominant females, of which the first two were accompanied resp. by an old juvenile female and an old juvenile male.
The females 3 and 5 are non-dominant females without offspring.
B = birth
? = observations not continued

food shortage it should be unfavorable for females to come in estrus because of the reduced frequency of encountering males and the energy demand caused by early pregnancy.

Males did appear to maintain consortship with receptive females, in general not for the entire period of estrus, but at least for periods of time ranging from one to three days and nights. Also, consortship between two males and a receptive female has been observed in <u>Ateles paniscus</u>, lasting sometimes over three days and nights.

Female advertisement was observed prior to all copulations (n = 27), concerning both non-dominant and dominant females. The receptive female always initiated sexual activity by fast moving towards a particular male and presenting her genitals, followed by sitting in his lap. When a male didn't react by initiating the copulatory position, the female rushed away through the tree crown, sat down somewhere else, and after several minutes could attempt a second or third time before the male locked his hindlegs around her torso. The consortship between one or two males and a receptive female usually did not take place secluded from the other members of the group, especially not in case of dominant females, but for copulating the pair could attempt to seek out seclusion, maybe because of strong interference from the side of a juvenile child. Several times, a receptive mother of a juvenile was observed separating from a subgroup just after entering a food tree, when the juvenile paid full attention to foraging. In these cases, the male immediately followed the female, and the pair copulated about 100 to 200 m away from the rest of the subgroup.

Receptive females appeared to choose a mate. Most obviously this was demonstrated, when a receptive female, ranging in a subgroup without males, reacted to male long calls by immediately altering the direction of travel, and rushing towards the calling male. After meeting him, advertisement and copulation followed. Once, a dominant female on the way to $♂_3$, calling before, about halfway encountered $♂_1$, advertised and copulated, but before ejaculation took place, broke off and rushed further towards $♂_3$, followed by a successful copulation.

The mean duration of observed copulations was 10 minutes. During copulation a female is very active, brings one hand to the abdomen, moves continuously to and fro on the branch on which the copulation takes place, shakes the head restlessly and regularly looks over the shoulder into the male's face. The lips are protruded and the eyes half-closed. Sometimes, the female rubs the male's upperleg or back with one hand. At the moment of ejaculation, the female may move a couple of meters with the male hanging behind her and then the animals separate.

In general, three or four copulations take place each day during a female's estrus period.

6.5. <u>Comparison of Spider Monkeys with Chimpanzees</u>

As already noted by Cant (1977), spider monkey social organization shows a remarkable similarity with that of the chimpanzee (<u>Pan troglodytes</u>). In Table 15, several features related to ecology, social organization and sexual behaviour are listed, for chimpanzees referring only to the more useful authors on the subject, for spider monkeys referring mainly to the present study on <u>Ateles paniscus paniscus</u>.

Both in spider monkeys and chimpanzees a highly developed knowledge of available food sources is present, and their detailed spatial memory results in economical routes between food sources. Apparently, both are capable of returning to certain food sources from any direction by routes as short as possible.

The loose, unstable social structure within the group (community) seems to be related to food specialism (especially ripe fruits) and seasonally varying food patch size, resulting in relatively large

Table 15. Spider monkeys compared with chimpanzees

Feature	Ateles	Pan
Over 50% frugivory; ripe fruits making up a considerable part of the diet (3,4,8,10)	+	+
Males perform food-calls (pant-hoots) (3,10)	+	+
Food-calling (pant-hooting) is negatively related to food supply (3,10)	+	+
Checking food sources soon becoming available (10)	+	+
Capacity for and continual use of a detailed spatial memory (10)	+	+
Distinguishable groups (communities) (3)	+	+
Intergroup agonistic behaviour (7,10)	+	+
Loose, unstable social structure within the group (community) (2,3)	+	+
Males travelling more extensively than females in times of great food supply (10)	+	+
Individual adults occupying 'core areas' within the group (community) range ('core area' referring to frequency of use of the area) (10)	+	+
Mean subgroup (party) size varying seasonally in relation to food supply (1,2,6,8,10)	+	+
Adult females more often ranging solitary than adult males (12)	+	+
Subgroup (party) size commonly small (2 - 3 animals) (3)	+	+
All-male subgroups (parties) (12)	+	+
All-female subgroups (parties) (12)	+	+
Male - male dominance (3,11)	+	+
Male - male cooperation in territorial defense (3,7,10)	+	+
Male relatedness in coalitions and territorial defense patrols (3,11)	+	+
Infrequent intragroup aggressive and submissive interactions (3)	+	+
Male - female consortship (9)	+	+
Female choice of mate and female advertising (9)	+	+
Female emigration (13)	+	+
Sexual dimorphism; males larger than females	slight	marked
Slow reproductive rate (3)	+	+
Predation very rare and mainly at night (10)	+	+

1. Azuma and Toyoshima (1962) - 2. Reynolds and Reynolds (1965) - 3. Goodall (1965, 1968) - 4. Napier and Napier (1967) - 5. Hladik (1973) - 6. Sugiyama (1973) - 7. Bygott (1974) - 8. Nishida (1974) - 9. Tutin (1975) - 10. Wrangham (1975, 1977) - 11. Riss and Goodall (1977) - 12. Halperin (1978) - 13. Pusey (1978)

subgroups (parties) in times of great food supply and relatively small ones in times of food shortage. The relation of body size with food patch size is reflected in a relatively high degree of solitariness, stronger so in chimpanzees, and relatively small subgroups (parties) throughout the year, the only permanent bonds formed by females with their offspring. Because of the flexible subgroup (party) size in both species, aggressive and submissive interactions within a group (community) are infrequent, and occur almost exclusively while feeding.

Individual adults occupy 'core areas' within the group (community) range, areas most frequently used in a particular part of the year. Male 'core areas' are larger than female ones, but at least in spider monkeys, females possess a better knowledge of available food sources within those areas. Adult females more often range solitary than males, possibly related to this knowledge.

Male - male dominance exists. Males cooperating in territorial defense patrols seem to be related. The fact that only females, and in spider monkeys especially young females, sometimes emigrate, contributes to the male relatedness within groups (communities).

As Wrangham (1975, 1977) points out for the chimpanzee, and it seems to be also applicable to spider monkeys, the sort of social system permits males to defend large territories, including ranges of several females, by cooperating in all-male parties during territorial defense patrols and, in case of spider monkeys, also by calling all group males to the spot in territorial boundary conflicts with other groups (communities). Hence, males seem to be able to defend more females than in cohesive bisexual groups like in many other primates.

7. POPULATION DYNAMICS

7.1. Home Range and Day Range Size

The annual home range of the spider monkey group in the Voltzberg study area covered 255 hectares, of which 220 offered suitable habitat in the form of high forest, high mountain savanna forest and pina swamp forest. The perimeter of its range was determined for a greater part by natural boundaries, like open granite, rocksavanna, low forest and liane forest, and where bordering the areas of neighbouring groups, its range appeared clearly-defined and non-overlapping.

Few estimates of home range size are available from other areas. Dare (1974) notes a range of 100 - 115 hectares for the A. geoffroyi group on Barro Colorado Island. Klein and Klein (1976) estimate ranges of 259 - 388 hectares with 20 - 30% overlap for A. belzebuth in La Macarena National Park in Colombia.

Travel distances from day to day were highly variable for A. paniscus in the Voltzberg study area, depending on the subgroup size and composition, the weather and the season, and the distribution patterns of particular food plants. Straight line distances between the consecutive food sources and sleeping trees used in one day could range from 500 meters (e.g., a solitary ranging male or non-dominant female during the dry season) to 5,000 meters (e.g., a subgroup led by a dominant female during the wet season).

Klein (1972) gives minimal distances traversed daily ranging from 483 to 1,770 meters, and estimates the upper range of straight line distances as large or larger than 4,000 meters. For A. geoffroyi on Barro Colorado Island also a high upper range of about 3,000 meters is given (Richard, 1970).

7.2. Population Density and Biomass

Because of its flexible grouping behaviour, in Ateles accurately estimating of group size, group composition and population density is only possible if the members of a group are recognizable individually.

In the Voltzberg study area, A. paniscus occurs at a density of 7.1 individuals or 6.3 independently locomoting individuals per km^2.

Considering only the area of suitable habitat, a density of 8.2, resp. 7.3 individuals per km^2 is calculated. The figures from other areas vary considerably, but only the estimate of Klein and Klein (1976) is based on individually recognizable animals of a natural population. Muckenhirn, et al. (1975) estimate 2.4 - 6.2 individuals per km^2 for *A. p. paniscus* in Guyana; Heltne, et al. (1975) give 2.0 individuals per km^2 for *A. p. chamek* in Bolivia; Klein and Klein (1976) give a density of 12 - 15 individuals of one year or older per km^2, and including infants 15 - 18 individuals per km^2 for *A. belzebuth* in Colombia; Bernstein, et al. (1976) estimate 9 - 14 individuals per km^2 in northern Colombia; Freese (1976) found 6 - 9 *A. geoffroyi* per km^2 in Costa Rica.
Much higher densities are given for *A. geoffroyi* in Guatemala, where Coelho, et al. (1976) estimated 45 individuals per km^2 and Cant (1977) 26 individuals per km^2. In Peru, Janson (1975) estimated 24 *A. p. chamek* per km^2.

The biomass for *A. paniscus* in the Voltzberg study area is calculated using the mean body weight data derived from Mittermeier (1977): 7.86 kg for males and 7.69 for females. The figures range between 0.4 and 0.5 kg/ha, depending on the home range size choosen (255 and 220 hectares, resp.). Estimates from other areas are the following: 0.3 - 0.5 (Freese, 1976), 0.07 (Eisenberg and Thorington, 1973), 0.7 (Bernstein, et al., 1976), 0.6 - 0.9 (Klein and Klein, 1976), 1.4 - 1.9 (Janson, 1975), 0.2 (Heltne, et al., 1975), and 0.3 - 0.6 kg/ha (Muckenhirn, et al., 1975).

7.3. Relationships with Other Animals

Polyspecific associations between *Ateles* and other monkeys were rarely seen and obviously were due to chance. Solitary ranging *Chiropotes* sometimes associated peacefully with a spider monkey subgroup for a while, possibly to learn from the spider monkeys about food sources. Furthermore, a juvenile spider monkey once left a subgroup, which included his mother and an adult male, and joined a group of 20 bearded sakis (*Chiropotes*) about 100 m away. While the adults waited, constantly trying to attract him by means of contact vocalizations, the juvenile played for about 15 minutes on end with a juvenile *Chiropotes*, before returning. Simple curiosity and/or desire to play should probably be regarded as companionship.
A male juvenile-2 spider monkey caught by hunters was released shortly after outside the Voltzberg study area. A year later, he was encountered several kilometers further and observed for some time in companionship with a small group of howler monkeys. The animal was feeding on partly different food sources but followed the howlers when moving, and was seen playing with the juvenile *Alouatta* in the group.
Klein and Klein (1973) report on occasional associations between *Ateles belzebuth* and *Alouatta seniculus* in Colombia and suggest that they resulted from similar resting, travelling and feeding preferences.
In the Voltzberg study area, however, part of the sleeping trees of *Ateles* were used also by *Alouatta* , but never at the same time. *Alouatta* seemed to avoid *Ateles*, and several times juvenile spider monkeys, sometimes in cooperation with adults, were seen chasing howlers playfully and biting their tail, when both were moving simultaneously towards the same sleeping tree preferred for the night. In these cases, the howlers travelled further being content with another tree nearby.

In addition to these few arboreal associations, several large, primarily terrestrial birds, like curassows (*Crax alector*) and trumpeters (*Psophia crepitans*), seemed to focus on foraging spider monkeys in order to feed on fruits dropped to the ground (see chapter 4.1.1.). Also, terrestrial mammals could be attracted by the noisy foraging spider monkeys in order to feed on the fruits and seeds dropped to the ground, like *Dasyprocta*, *Myoprocta*, *Tayassu*, *Mazama* and *Tapirus*. These associations are similar to the one described for *Alouatta palliata* and *Tayassu*

tajacu and *Dasyprocta punctata* observed visiting fruiting trees occupied by *Cebus capucinus* (Oppenheimer, 1968).
Most of these associations have ecological importance and are advantageous to one or both of the participant species. The terrestrial animals mentioned above, may feed on fruits otherwise not available to them and the spider monkeys may benefit from the alarm calls given by fleeing terrestrial animals when human intruders or possibly larger carnivores are coming into the area.

8. CONSERVATION

Spider monkeys are threatened by hunting, habitat destruction and live capture. *Ateles* is extremely vulnerable to hunting for several reasons. Locally it forms an important food item, since it is large, good to eat and easy to track. It defends itself against human intruders by an aggressive branch-shaking and branch-breaking display, giving the hunter the opportunity to shoot a whole subgroup out of a tree. Furthermore, it has a very low reproductive rate. Females do not give birth before their fifth year and later only to one infant every three to four years. Unfortunately, also its social structure makes it vulnerable to hunting, since the survival of the group as a whole may well depend on the temporal and spatial knowledge of food sources to be found in a certain area, stored in the heads of a few dominant females. For purposes of life capture, particularly the females carrying infants will be shot. Finally, the population density is rather low (7.1 individuals per km^2).

Habitat destruction is another threat to the spider monkey's survival. *Ateles* is largely restricted to the undisturbed, most heterogeneous high forests, which are going to disappear quickly all over its range. Based on forest type breadth, niche breadth of *Ateles* in Surinam is the lowest of all Surinam primate species (Mittermeier, 1977).

In general, it may be clear that *Ateles* is an extremely vulnerable species, showing little or no adaptability to human intrusion.
Despite local habitat destruction and hunting pressure, especially taking place along the main rivers, still most of the Surinam interior is undisturbed, making the outlook for conservation of several species, that are rapidly disappearing in large parts of Amazonia, fairly good. At the moment, Surinam parks and nature reserves protect as much as 5,304 km^2 of rain forest habitat in the interior, most of them in remote, uninhabited areas. When the infrastructure of the interior will be improved in the near future, the protection of these areas will be a major problem for conservationists. Hunting pressure will increase and also lumber extraction will threaten the areas. Unfortunately, many tree species providing spider monkeys, among other animals, with sleeping sites and food, produce commercially valuable timber.This disadvantage perhaps may be turned into an advantage, when the interests for both parties concerned can be combined in one project, as suggested below. The national parks and nature reserves will be best protected when surrounded by so-called buffer zones, where for instance lumber extraction may be managed in an appropriate and responsible way. To make this economically attainable, the density of commercially valuable tree species should be improved.
As pointed out before, specialized frugivores play an important, possibly vital role in the dispersal of a lot of plant species, in particular canopy trees with relatively large seeds protected against predation by either toxic compounds or a tough endocarp. In the Voltzberg study area, it seemed to be likely that spider monkeys had been the principal factor in the realization of locally high densities for species like *Virola melinonii*, *Guarea grandifolia*, *Ecclinusa guianensis*, *Capparis maroniensis*, *Tetragastris* spp., *Protium* spp. and *Ephedranthus guianensis*.

So, locally high densities of certain tree species do exist within the framework of primeval rain forest.
The above mentioned examples, considering spider monkeys as principal dispersal agents responsible for their locally higher densities, may be supplemented by another example considering a terrestrial seed predator.
The local abundance of the '*boegroemaka*' palm (*Astrocaryum sciophilum*) in the Raleighvallen-Voltzberg Nature Reserve may be correlated with the high density of scatter-hoarding agoutis, that belong to the principal terrestrial seed predators of the thick-walled kernels produced by this palm and dropped in quantities under the parent tree. By satiating the seed predator in this way, part of the palm-seed crop is burried by it. At least some of these storage places are not rediscovered by the animal or opened up too late, giving some seeds the opportunity to germinate. Buried in this way, the seeds effectively are protected against predation by bruchid weevils. In contrast, all kernels lying exposed on the forest floor appear to be either predated by agoutis or contain a little hole, demonstrating a larva of these bruchid weevils already has settled down in the endosperm.
In the Kayser Mountains, similar high densities of the '*bergimaripa*' palm (*Attalea speciosa*) were found in correlation with abundant scatter-hoarding agoutis and acouchis.

The balance between seed dispersers and seed- and seedling predators, as they interact with fruits, and the interaction between seed predators and wind-dispersed seeds, in my opinion seem to be the major processes in the production of a generally heterogeneous high rain forest, as it is when undisturbed. In this view, efforts should be made to influence the outcome of this balance in favor of certain commercially valuable timber species producing food for the animals, for instance by protecting the fauna, in particular the dispersal agents. In addition, selective cutting of saplings belonging to tree species worthless for both parties concerned could be carried out.
For many tree species terrestrial seed predators and herbivores focusing on beds of seeds and seedlings seem to be as important as their dispersal agents. For each species a minimal distance from the parent tree must exist, at which distance a solitary dropped seed has a fair chance not to be detected and destroyed in the stage of either seed or seedling.

Increase of density for several tree species in a given area must be realizable and may well be accompanied with higher densities of arboreal frugivores, terrestrial seed predators and herbivores. Since the latter category offers most of the important game species to local people, some game cropping of these animals within the buffer zones might be sustained.
The only realistic way to save at least part of the tropical rain forests for the future seems to be the combining of concerns to both conservationists and governments, logging companies, local people, recreants, etc., as may be exemplified above.

9. DISCUSSION

In the present study feeding behaviour is quantified using the relative frequency with which spider monkeys choose different foods. Instead, many observers use recording at fixed time intervals or the percentage of total feeding time for each food. Hartley (1953) used the method of relative frequency to estimate how much time titmice spent feeding in each food tree species, and pointed out the disadvantage of the method in being biased towards small trees only visited shortly. The method used in the present study may be liable to bias concerning food species that tend to grow in clumps and to widely dispersed ones. For example, *Virola* melinonii is evenly distributed throughout the study area but at high density, which may give a clumped appearance locally. The fruit crops of individual trees of this species usually differ much, some trees do not fruit every year, others alternate good crops with minor ones. Because of high density of Virola, a spider monkey subgroup may visit trees offering a small crop of ripe fruits that might not have exploited by then, when more dispersed, considering the fact that an itinerary choosen by a dominant female leading a subgroup appears to be straight-lined and highly economic, showing no inroads towards food sources of minor interest. However, examples of clumped food sources of one species are few in undisturbed high forest. Also, the widely dispersed food species will not be biased much in this method, because they will be incorporated in an economic route, and the kind of preferred food (nutritious mature fruit) does not sustain spider monkeys to feed on it with longer feeding bouts. In other words, the distance travelled to feed on dispersed food sources of the same species can not be compensated by much longer feeding bouts on each, like in the case of flush leaves or mass-ripened fruits.

In order to check the recording method, it is compared with that of calculating the percentage of total feeding time (Van Roosmalen, in prep.), which in turn has its own disadvantages, and yields no major differences. An important advantage of the method used, may be the complete dietary picture given, and the possibility to incorporate data from dung samples so important in the spider monkey, since it swallows seeds of almost every fruit species consumed and defecates them intact and identifiable.

Spider monkeys are extremely selective in their choice of food, and it differs little between either individuals or neighbouring groups, although dominant females appear to feed on more food items daily. These food items are recognized as food also by the other group members, but their obscure feeding sites are better or exclusively known to dominant females. Many nutritious foods are relatively uncommon or even rare, but they are selected to exploit on a regular base, sometimes using extended day ranges.

The abundance of certain preferred food spread over the year may impose a limit on population density, since the overall impression was that the potential of preferred food in the area was not much greater. The density and distribution patterns of food species as given in the appendix will not give a decisive answer on food availability, since individual fruit cropping within a species appeared to be very variable in terms of the amount of fruit offered, and the cycle of successful cropping. Obviously, while most food species were fruiting yearly, the individual fruiting trees used by the spider monkey group during the period January - May, 1978 were largely different from those of the corresponding species used during the same period in 1977, showing the overall pattern that many individual trees alternate good fruit crops with minor ones on a regular base. This was ascertained by marking exploited food trees with plastic tape and numbered tags for more than two years.

The overall impression that preferred food (nutritious fruits) is limiting population density in spider monkeys is based upon the phenomenon that during extensive wandering through the home range of the study group almost never trees were encountered which were not exploited by at least part of the group, while offering enough preferred food to the monkeys. This phenomenon was strongest so during the long dry season, a period of low fruit supply.

Seasonal variation in feeding on fruits, flowers and flush leaves obviously is related to changes in availability. When supply of preferred nutritious fruits is high, feeding on flush leaves and flowers is rare, while supply of the latter is low too. When supply of flush leaves and flowers is high, the availability of nutritious fruits is low and consequently the rate of feeding on flush leaves and flowers is relatively high. On account of the total number of food items available both in November and December, a food excess seems to exist, but the supply of preferred fruits is still low and the overall quality of food has probably declined. During the long dry season, when the supply of nutritious fruits is low, spider monkeys appear to be very dependent on a few nutritious fruit species, and failure in cropping of one or more of these species once in several years or longer, may cause mortality by making the weaker, less fed animals more sensible to parasites and fatal diseases. Mortality among adult males may be higher at these instances because of their less developed ecological knowledge and their larger ranges than females usually have.

Social organization like in spider monkeys appears to make the population more flexible in overcoming the problem of seasonal shift in fruit abundance and sometimes even food shortage. Its social system seems to have coevolved with its food specialism and implicit feeding behaviour. It may have evolved from a partly or largely folivorous to a specialized frugivorous monkey, parallel with its locomotory evolution to a quadrumanous climbing, forelimb-dominated locomotion during feeding (in twig habitat where most fruits are to be found) that is considered the primary hominoid adaptation (Fleagle, 1976).

Spider monkey food specialism concerns nutritious, mostly large-seeded, mature fruits, which as a rule are available for relatively long periods of time, but in small amount at a time within one food plant. This type of fruit seems to have coevolved with specialized frugivorous animals feeding on it and providing the plant species with high-quality dispersal. These plants invest much more energy per propagule than for example small-seeded berries, figs, or wind-dispersed fruits do, which species generally produce mass-ripened crops in order to satiate terrestrial seed predators, and use a wide array of dispersers opportunistically feeding on these fruits. High quality of dispersal offered in this type of fruit by for instance spider monkeys, implies a reliable visitation for prolonged periods of time (to be expected when these fruits are worthwhile to feed on), a gentle treatment by its mouth and gut, in case of stones implicating quicker germination after defecation, endozoochorical transport over considerable distances from the parent tree, dropping in preferred habitat and development of relatively large seeds containing more endosperm, which increases the chance of successfully overcoming the first stage in the life cycle of a plant as seedling. This strategy has many advantages for the plant but costs are high considering that the soil covered by tropical rain forest, in general, is poor in anorganic compounds and minerals. This might have been the major reason for many high forest plants with this type of fruit to produce asynchronous, slow-ripening and not yearly successful fruit crops favouring both the specialized frugivorous animals and its own dispersal. In fact, few fruits of the nutritious type are dropped unexploited on the forest floor under the parent tree. They are exploited in a regular and economic way by specialized frugivores depending largely on them. This may be also an explanation why so many terrestrial animals do focus on foraging spider monkeys, competing with one another for being the first to reach the feeding site, because otherwise these nutritious fruits are hardly obtainable for them.

Prolonged, asynchronous, slow-ripening fruit crops, providing small amounts of mature fruits at any given time, force large-sized specialized frugivores, like spider monkeys are, to forage in small parties and with relatively short feeding bouts. In contrast, another sympatric monkey, the bearded saki (*Chiropotes satanas chiropotes*), showing about similar habitat preferences (like horizontal and vertical distribution) (Van Roosmalen, Mittermeier and Fleagle, in press), but feeding largely on immature seeds, with ripe fruits and flowers playing an insignificant role in the diet, shows a completely different social organization and foraging strategy, while overlap in the choice of food species between both monkeys is considerable. The bearded saki forages in large, one- or two-male groups (8 - 30+ animals) and ranges over large areas, while foraging routes appear to be largely determined by spatial distribution of certain vegetation types, subtypes or phytosociological units of lower rank, offering relatively high densities of few species with edible young seeds. Since the stage of immaturity appears not critical to the monkey, seeds are available for many months and in large quantities within one food source. This makes possible to forage in large groups. Also, there is some seasonality in the supply of young seeds. If certain vegetation types or plant associations do not offer enough to feed on together, during the course of a day's foraging activities a group may break up into two or three subgroups spread over a large area, but constantly keeping mutual contact by means of loud vocalizations. However, sleeping and travelling between foraging grounds is performed cohesively by all group members.

This comparison of two sympatric primate species, largely overlapping in habitat choice and choice of food species, examplifies that social organization among primates may be related to very fine interspecific ecological differences such as diet in terms of fruit species preferred to be eaten in different stages. Attempts to relate interspecific differences in social organization among primates to gross ecological differences is foredoomed to failure, since differences within groupings formed in this way appear to be more impressive than differences between them. Therefore, more autecological field studies are needed, in particular describing diet and phenology of food plants in much more detail than usually is done.

10. SUMMARY

This study describes habitat choice of the Surinam black spider monkey (Ateles paniscus paniscus) and clarifies complex temporal and spatial effects of food sources on the behaviour of a group of spider monkeys in a 350 ha study area in central Surinam in terms of food category, food plant identity and phenology, and in terms of quantity, density and dispersion of the most important of these food sources. It recognizes the fundamental importance of mature-fruit feeding to spider-monkey foraging strategy and discusses implications of diet to social behaviour.
From a conservational point of view, this study is essential in emphasizing the extreme vulnerability of the spider monkey to both hunting and habitat destruction, and in providing detailed information on its habitat choice and dietary requirements, so urgently needed in order to assess in a responsible way the site of areas to protect and the potential of already preposed protected areas. The spider monkey may serve as an important 'indicator' species, reflecting the degree of disturbance of Amazonian tropical rain forests.

1,2,3. Among the eight Surinam monkey species, Ateles p. paniscus is the most restricted in habitat. In the Voltzberg region, it occurs exclusively in high forest (92.6%), infrequently enters edge habitats (14.9%) and is found primarily in the upper levels of the canopy and in emergents (72.3%). The understory is rarely used (0.8%), and the lower extreme of its vertical range appears to be 12 meters.
Among the seven major forest types available in the Raleighvallen-Voltzberg region, spider monkeys are observed only in high rain forest, mountain savanna forest, pina swamp forest and riverbank high forest.

4. A total of 207 food plant species are used, of which 68.1% trees. Most important families, providing the monkeys with food, are Moraceae and Mimosaceae, regarding both the number of food species and the percentage of total feeding records.
Ateles p. paniscus is mainly frugivorous, feeding on 171 species of fruit, 33 species of flower and 28 species of leaf. Mature fruit makes up 96% of the total number of fruit feeding records. The occasional feeding on insects (termites and caterpillars) definitively has been ascertained. The average annual food intake is 82.9% fruits, 6.4% flowers, 7.9% flush leaves, 1.7% bark and 1.0% miscellaneous (e.g., rotten palm-sheaths, pseudobulbs, aerial roots, honey, insects). The monthly variation in food choice shows a strong correlation with the phenology. During the first part of the long dry season (July - September), a period of low fruit supply, the monkey compensates its diet with relatively high percentages of both flowers and flush leaves, while during the long wet season (March - June) fruit abundance causes very low percentages of both flowers and flush leaves in the diet. The percentages are strongly determined individually by its supply in relation to the ecological change, but ripe fruits always are preferred above all.
Young seeds play a minor overall role in the diet, except during the period May - June. By ingesting large quantities of young seeds, rich in protein and fat, during the peak of the long wet season the monkeys seem to stock up on energy for the coming months of food scarcity (July - October).
Ateles appeared to play an important role as dispersal agent for many plant species, and for some species it seemed to be the only disperser. Endozoochorical seed dispersal by spider monkeys took place in 138 plant species (accounting for 93.5% of total fruit feeding records), seed dropping was recorded in 10 species (2.7%) and seed predation in 23 species (3.7%). Ateles belongs to the category of 'specialized frugivores', who derive all or most of their supplies of carbohydrate, lipid and protein from fruits. Large-seeded,nutritious fruits seem to have coevolved with specialized frugivores as their principal dispersal agents, resulting in a greater quality of dispersal than can be seen in small-seeded, low-nutritious fruits dispersed by a wide array of both 'opportunistic' and 'specialized' fruit-eating animals. This coevolutionary pattern (the high nutritive content of the flesh in large-seeded fruits) may be demonstrated in families such as Palmae, Burseraceae, Myristicaceae, Sapindaceae, Loganiaceae, Capparaceae, Sapotaceae and Meliaceae, all producing important fruits for spider monkeys. Among 166 plant species producing edible fruits, used by the spider monkeys in the Voltzberg region, about 80% is nutritious and large-seeded. Low-nutritious, small-seeded fruits (especially berries and figs), making up only 20%, were exploited only incidentally on the way from one nutritious fruit source to another, and almost never appeared to influence the daily foraging routes nor were revisited regularly. These species often produce mass-ripened fruit crops on which the monkeys cannot depend much. The fruiting seasons of the former category, however, in general last relatively long because of more or less asynchronous fruit-maturing within and between individuals of the species, apparently since the small number of specialized dispersal agents may be easily overloaded. The competition between these plant species for the high-quality dispersal offered by a small number of dispersers may have evolved in elongated and displaced, but broadly overlapping fruiting seasons as required for the existence of specialized frugivores.

5. Foraging behaviour in spider monkeys is differing strikingly with the seasons. During the long wet season, when fruit is abundant, activity budgets are increased resulting in large day ranges (with a maximum of 5,000 meters), prolonged feeding times, short resting times and many

food sources (especially mature fruits) exploited daily. Foraging often takes place in relatively large subgroups breaking up and reassembling regularly, the subparties using partly different food sources but following about similar itineraries.

During the long dry season, when fruit supply is low and a food scarcity or even a food shortage may exist, activity budgets are lowered to a minimum, resulting in short day ranges (with a minimum of 500 meters), prolonged resting times and short feeding times (few relatively long feeding bouts), few food sources exploited daily and diet composition differing in much higher percentages of flowers and flush leaves. Finally, mean subgroup size is decreased strongly.

Spider monkeys live in medium-sized groups fragmenting into widely dispersed subgroups of varying composition. Daily itineraries and activity patterns of a subgroup mostly are determined by a so-called dominant (usually aged) female with or without offspring, or sometimes by two dominant females alternately. These females appear to possess the best knowledge of certain parts of the group's range, the so-called core areas, and are capable of preplanning an economic foraging route for the day along as much as 8 to 30 different food sources. By checking regularly potential food sources on their stage of maturing and using a highly developed spatial and temporal memory, these females are able to incorporate these food sources in their foraging routes just after becoming available. The interval between subsequent visits to a particular food source appears to be species specific, depending on the rate of fruit maturing. In some species the last stage of maturing is going fast, offering the monkeys every day enough ripe fruits to feed on together. Many species, however, are exploited in a 2 - 4 days cycle, some in a 5 - 8 days cycle or even more.

Spider monkeys appear to select for variety, using on average about 14 different food items daily, making up about a quarter of the average monthly number of food items used. Among these, 3 or 4 food items are most important considering the amount of feeding time and the estimated total weight of food ingested.

6. A group of Ateles p. paniscus usually consists of 15 - 20 individuals, although they may never be observed all together at the same place.

A group fragments into several subgroups of varying composition, a female with offspring of an age ranging from 0 to about 5 years being the only persistent bond.

Sex ratio of adult males to females is 1 : 2(-3). The adult males of a group appear to defend a territory with clearcut boundaries, while females sometimes visit neighbouring groups and even may emigrate.

Spider-monkey social system is characterized by its flexible grouping behaviour and seems to be coevolved with the species food specialism concerning mainly nutritious, large-seeded fruits. The supply of this type of food is varying strongly with the seasons and maturing within and between individual fruiting plants, in general, is rather slow and asynchronous. Moreover, individual mature fruits of this type are shortly available to the monkey. After becoming mature, most fruits soon drop to the ground or when dehiscent, become available to birds. For more than three large-sized spider monkeys these food plants seldom offer enough to feed on together and to make the visit worthwhile in terms of energy expenditure. Consequently, subgroups consisting of three or less individuals are encountered most often throughout the year. However, the high density of particular food plants fruiting during the long wet season, makes it possible for spider monkeys to forage in much larger subgroups, often containing two dominant females and ranging in size up to 9 individuals, using simultaneously about the same itineraries, but exploiting partly different food sources. As a result, during this season intragroup social interactions are more frequent.

During the following long dry season, when nutritious fruits are scarse and some years even a severe food shortage may exist, the mean subgroup size decreases strongly, in particular effectuated so by the splitting of dominant-female core areas, which show almost no overlap anymore. Non-dominant females and males still may join subgroups led by a dominant female to share ecological knowledge of food sources, but they do so less frequently. Day ranges drop strikingly and the animals are more silent, both factors contributing to the lower chance of encounter. Activity budgets are decreased, in particular in males and non-dominant females. The better knowledge of available food in dominant females may favour them especially during the long dry season. This may be a reason that dominant females seem more successful in rearing offspring than non-dominant females, and perhaps that mortality in adult males seems higher considering the sex ratio.

At the end of the long dry season, when preferred fruit is still low in supply, the relatively frequent feeding on flush leaves and flowers, again, sustains foraging in larger subgroups, because of the great amount of food offered at the same time and by mostly large-crowned, flushing or blooming food plants.

Adult males do have core areas, which are larger than dominant-female core areas and even may combine those of two dominant females.

They cooperate in territorial defense patrols and long distance agonism in case of boundary conflicts. In this way, spider-monkey males seem to be able to defend more females than they should in a social system with cohesive bisexual groups, like in many other primates.

Spider-monkey social system is unusual among primates and only shows striking similarities with that of the chimpanzee (Pan troglodytes). Both species are largely frugivorous, and show a loose, unstable social structure within distinguishable groups. Subgroup size varies seasonally in relation to food supply and most commonly is small. Individual adults occupy 'core areas' and show capacity for and continual use of a detailed, high developed spatial memory. Also dominance behaviour and sexual behaviour show remarkable similarities between both species.

7. The annual home range of the spider-monkey study group in the Voltzberg study area covered 255 hectares, of which 220 hectares offered suitable habitat. Day range size ranged between 500 and 5,000 meters, depending on the subgroup size and composition, the weather, the season and the distribution of particular important food sources. In the Voltzberg region, Ateles p. paniscus occurs at a density of 7.1 individuals per km^2, or 8.2 individuals per km^2 when only suitable habitat is considered. Biomass is ranging between 0.4 and 0.5 kg/ha, depending on the home range figure choosen.

Ateles does not show polyspecific associations with other sympatric primate species. Some short-term associations observed were due to chance or should probably be regarded as companionship. Associations with terrestrial birds and mammals, however, are frequently observed and may be advantageous for one or both of the participant species. The terrestrial animals focus on the noisy foraging spider monkeys to obtain nutritious fruits and/or seeds immediately after dropping, while alarm calls emitted by fleeing terrestrial animals may benefit the spider monkeys, warning them against possible intruders coming into the area.

8. Spider monkeys are extremely vulnerable to hunting and habitat destruction. All over their range they disappear in the face of human entrance, showing little or no adaptability to human intrusion.

Emphasizing the important role of specialized frugivores, like spider monkeys, as dispersal agents for many rain forest plants, and the balance between seed dispersers and seed- and seedling predators as they interact with fruits, having a strong impact on structure and composition of primeval tropical rain forest, a suggestion is made to combine interests of both conservationists and exploiters of rain forest treasures in conservational projects, like that of a responsible exploiting of buffer zones surrounding national parks and nature reserves, by increasing density of particular commercially valuable and edible fruit producing trees, and sustaining restricted game cropping of terrestrial seed predators and herbivores, like agoutis, acouchis, peccaries, deer and tapirs.

- - -

REFERENCES

Azuma, S. and Toyoshima, A. (1962). Progress report of the survey of chimpanzees in their natural habitat, Kabogo Point Area, Tanganyika. Primates 3: 61-70.

Bakker, J.P. (1957). Quelques aspects du problème des sédiments corrélatifs en climat tropical humide. Zeitschr. f. Geomorph. 1: 1-43.

Bakker, J.P. (1957). Zur Entstehung von Pingen, Oriçangas und Dellen in den feuchten Tropen, mit besonderer Berücksichtigung des Voltzberggebietes (Surinam). Abh. Geogr. Inst. d. Fr. Univ. Berlin, 5: 7-20.

Beard, J.S. (1955). The classification of tropical American vegetation types. Ecology 36: 89-100.

Bernstein, I.S., Balcaen, P., Dresdale, H., Gouzoules, H., Kavanagh, M., Patterson, T. and Neyman-Warner, P. (1976). Differential effects of forest degradation on primate populations. Primates 17: 401-411.

Braak, C. (1935). Het klimaat van Nederlandsch West-Indië. Kon.Ned.Met. Inst. 1-2, Med.en Verh.36: 1-120.

Bygott, J.D. (1974). Agonistic Behaviour and Dominance in Wild Chimpanzees. Ph.D.thesis, University of Cambridge.

Cant, J.G.H. (in press). Population survey of the spider monkey *Ateles geoffroyi* at Tikal, Guatemala. Primates.

Cant, J.G.H. (1979). Dispersal of *Stemmadenia donnel-smithii* by birds and monkeys. Biotropica 11: 122.

Carpenter, C.R. (1935). Behavior of the red spider monkey (*Ateles geoffroyi*) in Panama. J.Mammal.16: 171-180. (also in C.R.Carpenter, *Naturalistic* Behavior of Nonhuman Primates).

Chivers, D.J. (1969). On the daily behaviour of howling monkey groups. Folia primatol.10: 48-102.

Chivers, D.J. (1974). The siamang in Malaya: a field study of a primate in tropical rain forest. Contr. to primat.4: 1-335. Karger, Basel.

Chivers, D.J. (1977). The feeding behaviour of siamang (*Symphalangus syndactylus*). In: Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes (T.H.Clutton-Brock, ed.), Academic Press, London.

Clutton-Brock, T.H. (1975). Feeding behaviour of red colobus and black and white colobus in East Africa. Folia primat.23: 165-207.

Clutton-Brock, T.H. (1977). Some aspects of intraspecific variation in feeding and ranging behaviour in primates. In: Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes (T.H. Clutton-Brock, ed.), Academic Press, London.

Clutton-Brock, T.H. (1977). Methodology and measurement. Appendix 1. In: Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes (T.H. Clutton-Brock, ed.), Academic Press, London.

Clutton-Brock, T.H. and Harvey, P.H. (1977). Species differences in feeding and ranging behaviour in primates. In: Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes (T.H. Clutton-Brock, ed.) Academic Press, London.

Coelho, A.M. (1974). Socio-bioenergetics and sexual dimorphism in primates. Primates 15: 263-269.

Coelho, A.M. (1975). Social organization and resource availability in Guatemalan howler and spider monkeys: a sociobioenergetic analysis. Paper presented at the 44th Annual Meeting of the American Association of Physical Anthropologists, Denver, Colorado.

Coelho, A.M., Bramblett, C.A., Quick, L.B. and Bramblett, S.S. (1976). Resource availability and population density in primates: a sociobioenergetic analysis of the energy budgets of Guatemalan howler and spider monkeys. Primates 17: 63-80.

Collin, C.D.(1822). Fauna Surinamensis. Thesis, Upsala.

Cruz Lima, E. da (1944). Mamiferos da Amazonia. Introdução Geral e Primatas. Museu Paraense Emilio Goeldi de Historia Natural e Ethnografia, Belem do Para, Brazil.

Dare, R. (1974). The social behavior and ecology of spider monkeys, *Ateles geoffroyi*, on Barro Colorado Island. Unpublished doctoral dissertation, Univ. of Oregon.

Dare, R. (1974). Food-sharing in free-ranging *Ateles geoffroyi* (red spider monkeys). Lab.Prim.Newsl.13(1): 19-21.

Dare, R. (1975). The effects of fruit abundance on movement patterns of free-ranging spider monkeys, *Ateles geoffroyi*. Paper presented at meeting of Amer.Assoc. of Phys. Anthrop. Denver, Colorado, April 9-12. Abstract in Amer.J.Phys.Anthrop.42: 297.

Durham, N. (1971). Effects of altitude differences on group organization of wild black spider monkeys (*Ateles paniscus*). Proc.Third Int.Congr. Primatol. (Zürich): 32-40.

Durham, N. (1975). Some ecological, distributional and group behavioral features of Atelinae in southern Peru, with comments on interspecific relations. In: Socioecology and Psychology of Primates (R.A. Tuttle, ed.), Aldine, Chicago.

Eisenberg, J.F. (1973). Reproduction in two species of spider monkeys, *Ateles fusciceps* and *A. geoffroyi*. J. Mammal.54: 955-957.

Eisenberg, J.F. (1976). Communication mechanisms and social integration in the black spider monkey, *Ateles fusciceps robustus*, and related species. Smithson.Contrib.Zool.213: 1-108.

Eisenberg, J.F. and Kuehn, R. (1966). The behavior of *Ateles geoffroyi* and related species. Smithson. Misc. Collns.151(8): 1-63.

Eisenberg, J.F., Muckenhirn, N.A. and Rudran, R. (1972). The relationship between ecology and social structure in primates. Science 176: 863-874.

Eisenberg, J.F. and Thorington, R.W. (1973). A preliminary analysis of a Neotropical mammal fauna. Biotropica 5(3): 150-161.

Fanshawe, D.B. (1952). The vegetation of British Guiana, a preliminary review. Imp. For. Inst. Oxf., Inst. Pap. 29.

Fanshawe, D.B. (1954). Forest types of British Guiana. Carib. For. 15: 73 - 111.

Fotogeologische Kaart van Suriname (1966). Ministerie van Opbouw, Paramaribo, Suriname.

Fooden, J. (1964). Stomach contents and gastro-intestinal proportions in wild-shot Guianan monkeys. Amer. Journ. Anthrop.22: 227-232.

Freese, C. (1975). A census of non-human primates in Peru. In: Primate Censusing Studies in Peru and Colombia, pp. 17-42, Pan American Health Organization, Washington, D.C.

Freese, C. (1976). Censusing *Alouatta palliata*, *Ateles geoffroyi* and *Cebus capucinus* in the Costa Rican Dry Forest. In: Neotropical Primates: Field Studies and Conservation (R.W. Thorington, Jr. and P.G. Heltne, eds.), pp. 4-9, National Academy of Sciences, Washington, D.C.

Freese, C. (1978). Population densities and niche separation in some Amazonian monkey communities. Diss. Abstr. Int. B38: 5732-5733.

Gautier-Hion, A. and Gautier, J.P. (1979). Ecological niche and species diversity in sympatric forest monkeys. Terre et la Vie 33: 493-507.

Geyskes, D.C. (1954). Het dierlijk voedsel van bosnegers aan de Marowijne. Vox Guyanae 1(2): 61-83.

Geyskes, D.C. (1957). Met de Oajana's op stap. Vox Guyanae 2(5-6): 193-300.

Geyskes, D.C. (1959). De Expeditie naar de Tafelberg in 1958. Vox Guyanae 3(4): 1-52.

Geyskes, D.C. (1970). Documentary information about the Surinam or Wama Indians. Nieuwe West-Indische Gids 3: 260-285.

Goodall, J. (1968). The behaviour of free-living chimpanzees in the Gombe Stream Reserve. Animal. Behav. Monogr. 1(3): 165-311.

Goodall, J. (1973). Cultural elements in a chimpanzee community. Symp. IVth Int. Congr. Primat. 1: 144-184. (Karger, Basel).

Haversmidt, F. (1967). The Birds of Surinam. (Oliver & Boyd Ltd., Edinburgh).

Heltne, P.G. and Kunkel, L.M. (1975). Taxonomic notes on the pelage of *Ateles paniscus paniscus*, *A.p.chamek* (sensu Kellogg and Goldman, 1944) and *A. fusciceps rufiventris* (= *A.f.robustus* Kellogg and Goldman, 1944). J. Med. Primatol. 4: 83-102.

Heltne, P.G. and Thorington, R.W. (1976). Problems and potentials for primate biology and conservation in the New World. In: Neotropical Primates: Field Studies and Conservation (R.W. Thorington, Jr. and P.G. Heltne, eds.), pp. 110-124, National Academy of Sciences, Washington, D.C.

Hernández-Camacho, J. and Cooper, R.W. (1976). The nonhuman primates of Colombia. In: Neotropical Primates: Field Studies and Conservation (R.W. Thorington, Jr. and P.G. Heltne, eds.), pp. 35-69, National Academy of Sciences, Washington, D.C.

Hershkovitz, P. (1949). Mammals of northern Colombia. Preliminary report no.4. Monkeys (Primates), with taxonomic revisions of some forms. Proc. U. S. Nat. Mus. 98: 323-427.

Hershkovitz, P. (1958). Type localities and nomenclature of some American primates, with remarks on secondary homonyms. Proc. Biol. Soc. Washington 71: 53-56.

Hershkovitz, P. (1969). The evolution of mammals on southern continents. VI. The recent mammals of the Neotropical region: zoogeographical and ecological review. Quart. Rev. Biol. 44: 1-70.

Hershkovitz, P. (1972). Notes on New World monkeys. Int. Zoo Yb. 12: 3-12.

Hershkovitz, P. (1977). Living New World monkeys (Platyrrhini)(Univ. of Chicago Press, Chicago).

Hill, W.C.O. (1962). Primates. Comparative Anatomy and Taxonomy. Vol. V. Cebidae, Part B. Univ.Press, Edinburgh.

Hladik, A. and Hladik, C.M. (1969). Rapports trophiques entre végétation et primates dans la forêt de Barro Colorado (Panama). La Terre et la Vie 23: 25-117.

Hladik, C.M. (1972). L'Atèle de Geoffroy, ce singe-araignée. Science et Nature 111: 1-11.

Hladik,C.M. (1975). Ecology, diet and social patterning in Old and New World primates. In: Socioecology and Psychology of Primates (R.H. Tuttle, ed.), pp. 3-35, Mouton Publishers, The Hague.

Hladik, C.M. (1977). Chimpanzees of Gabon and Chimpanzees of Gombe: some comparative data on the diet. In: Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes (T.H. Clutton-Brock, ed.), Academic Press, London.

Hladik, C.M., Hladik, A., Bousset, J., Valdebouze, P., Viroben, G. and Delort-Laval, J. (1971). Le régime alimentaire des Primates de l'île de Barro-Colorado (Panama). Résultats des analyses quantitatives. Folia primatol. 16: 85-122.

Hoogmoed, M.S. (1969). Notes on the herpetofauna of Surinam 1.- Itinerary of a herpetological collecting trip to Surinam in 1968. Zool. Meded., Leiden 44(4): 47-73.

Husson, A.M. (1957). Notes on the primates of Surinam. Studies on the Fauna of Suriname and other Guyanas 1: 13-40.

Husson, A.M. (1973). Zoogdieren van Suriname. Zool. Bijdr. 14.

Ijzerman, R. (1931). Outline of the geology and petrology of Surinam (Dutch Guiana), pp. 1-519.

Izawa, K. (1975). Foods and feeding behaviour of monkeys in the Upper Amazon Basin. Primates 16: 295-316.

Izawa, K. (1976). Group sizes and compositions of monkeys in the Upper Amazon Basin. Primates 17: 367-399.

Izawa, K., Kimura, K. and Nieto, A.S. (1979). Grouping of the wild spider monkey. Primates 20: 503-512.

Kappler, A. (1888). The monkeys of Dutch Guiana. Pop. Sci. Monthly 32(3): 396-400.

Kellogg, R. and Goldman, E.A. (1944). Review of the spider monkeys. Proc. U. S. Nat. Mus. 96: 1-45.

Kiester, A.R. and Slatkin, M. (1974). A strategy of movement and resource utilization. Theor. Pop. Biol. 6(1): 1-20.

Klein, L.L. (1971). Observations on copulation and seasonal reproduction of two species of spider monkeys, *Ateles belzebuth* and *A. geoffroyi*. Folia primatol. 15: 233-248.

Klein, L.L. (1972). The ecology and social organization of the spider monkey, *Ateles belzebuth*. Unpublished doctoral dissertation, University of California, Berkeley.

Klein, L.L. (1974). Agonistic behavior in neotropical primates. In: Primate Aggression, Territoriality, and Xenophobia: a Comparative Perspective (R. Holloway, ed.), pp. 77-122. Academic Press, New York and London.

Klein, L.L. and Klein, D.J. (1971). Aspects of social behavior in a colony of spider monkeys, *Ateles geoffroyi*, at the San Francisco Zoo. Int. Zoo Yb. 11: 175-181.

Klein, L.L. and Klein, D.J. (1973). Observations on two types of neotropical primate intertaxa associations. Am. J. Phys. Anthrop. 38: 649-653.

Klein, L.L. and Klein, D.J. (1975). Social and ecological contrasts between four taxa of neotropical primates. In: Socioecology and Psychology of Primates (R.H. Tuttle, ed.), pp. 59-85, Mouton Publishers, The Hague.

Klein, L.L. and Klein, D.J. (1976). Neotropical Primates: Aspects of habitat usage, [illegible] population density and regional distribution in La Macarena, Colombia. In: Neotropical Primates: Field Studies and Conservation (R.W. Thorington, Jr. and P.G. Heltne, eds.), pp. 70-79, National Academy of Sciences, Washington, D.C.

Klein, L.L. and Klein, D.J. (1977). Feeding behavior of the Colombian Spider Monkey, *Ateles belzebuth*. In: Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes (T.H. Clutton-Brock, ed.), Academic Press, London.

Klein, L.L., Klein, D.J. and Roosmalen, M.G.M. van (in press). Behavior and ecology of *Ateles*. In: Behavior and Ecology of Neotropical Primates (R.A. Mittermeier and A.F. Coimbra-Filho, eds.), Brazilian Academy of Sciences, Rio de Janeiro, Brazil.

Leeflang, E.C., Kolader, J.H. and Kroonenberg, S.B. (1976). Suriname in geografisch perspektief. Bolivar Editions, Paramaribo, Suriname.

Lenselink, J. (1972). De jachtopbrengst in een Surinaams Trio-dorp. De Surinaamse Landbouw 20(3): 37-41.

Lindeman, J.C. (1953). The vegetation of the coastal region of Suriname. The Vegetation of Suriname, Vol.1, part 1.

Lindeman, J.C. and Moolenaar, S.P. (1959). Preliminary survey of the vegetation of northern Suriname. The Vegetation of Suriname, Vol.1, part 2, pp. 1-45.

Milton, K. and May, M.L. (1976). Body weight, diet and home range area in primates. Nature 259: 459-462.

Mitani, J.C. and Rodman, P.S. (1979). The relation of ranging pattern and home range size to defendability, with an analysis of territoriality among primate species. Behav. Ecol. Sociobiol. 5: 241-251.

Mittermeier, R.A. (1977). Distribution, synecology and conservation of Surinam monkeys. Unpublished Ph.D. thesis, Harvard University, Cambridge.

Mittermeier, R.A. and Coimbra-Filho, A.F. (1977). Primate conservation in Brazilian Amazonia. In: Primate Conservation (G. Bourne and Prince Rainier of Monaco, eds.), Academic Press, New York.

Mittermeier, R.A. and Fleagle, J.G. (1976). The locomotor and postural repertoires of *Ateles geoffroyi* and *Colobus guereza*, and a reevaluation of the locomotor category semibrachiation. Amer. J. Phys. Anthrop. 45(2): 235-255.

Mittermeier, R.A. and Roosmalen, M.G.M. van (1980). Preliminary observations on habitat utilization and niche separation in Surinam monkeys. Biotropica.

Moynihan, M. (1976). The New World Primates. Princeton Univ. Press, Princeton, New Yersey.

Muckenhirn, N.A., Mortensen, B.K., Vessey, S., Fraser, C.E.O. and Singh, B. (1975). Report on a primate survey in Guyana, July-October, 1975. Pan American Health Organization.

Napier, J.R. and Napier, P.H. (1967). A Handbook of Living Primates. Academic Press, New York.

Neville, M.K. (1976). Census of primates in Peru. In: First Interamerican Conference on Conservation and Utilization of American Nonhuman Primates in Biomedical Research, Pan American Health Organization, pp. 19-29.

Neville, M.K., Castro, N., Marmol, A. and Revilla, J. (1976). Censusing primate populations in the reserved area of the Pacaya and Samiria Rivers, Department Loreto, Peru. Primates 17: 151-181.

Nishida, T. (1968). The social group of wild chimpanzees in the Mahali Mountains. Primates 9: 167-224.

O'Herne, L. (1966). A short introduction to the geology of Surinam. Geologisch Mijnbouwkundige Dienst, Ministerie van Opbouw, Paramaribo, Surinam.

Oppenheimer, J.R. (1968). Behavior and ecology of the white-faced monkey, *Cebus capucinus*, on Barro Colorado Island. Unpublished doctoral dissertation, Univ. of Illinois, 189 pp.

Reynolds, V. and Reynolds, F. (1965). Chimpanzees of the Budongo forest. In: Primate Behavior (I. DeVore, ed.). Holt, Rinehart and Winston, New York.

Richard, A. (1970). A comparative study of the activity patterns and behavior of *Alouatta villosa* and *Ateles geoffroyi*. Folia primatol. 12: 241-263.

Richards, P.W. (1966). The Tropical Rain Forest. Cambridge University Press, Cambridge.

Rodman, P.S. (1977). Diets, densities and distributions of Bornean primates. In: Arboreal Folivores (G.G. Montgomery and J.F. Eisenberg, eds.), Smithsonian Institution, Washington, D.C.

Rondinelli, R. and Klein, L.L. (1976). An analysis of adult social spacing tendencies and related social interactions in a colony of spider monkeys, *Ateles geoffroyi*, at the San Francisco Zoo. Folia primatol.25: 122-142.

Roosmalen, M.G.M.van (1977). Surinaams Vruchtenboek, 555 pp. Univ. of Utrecht.

Rossan, R.N. and Baerg, D.C. (1977). Laboratory and feral hybridization of *Ateles geoffroyi panamensis* Kellogg and Goldman 1944 and *A. fusciceps robustus* Allen 1914 in Panama. Primates 18: 235-237.

Sabater Pi, J. (1979). Feeding behaviour and diet of chimpanzees (*Pan troglodytes troglodytes*) in the Okorobiko Mountains of Rio Muni (West Africa). Zeitschr. fur Tierpsych. 50: 265-281.

Sanderson, I.T. (1939). A journey in Dutch Guyana. Geogr.Jour. 93(6): 468-490.

Sanderson, I.T. (1949). A brief review of the mammals of Suriname (Dutch Guyana), based upon a collection made in 1938. Proc. Zool. Soc. London 119: 755-789.

Sanderson, I.T. (1957). The Monkey Kingdom. Doubleday, Garden City, New York.

Schoener, T.W. (1971). Theory of feeding strategies. Ann. Rev. Ecol. Syst. 2: 369-404.

Schulz, J.P. (1960). Ecological studies on rain forest in northern Suriname. The Vegetation of Suriname (I.A. de Hulster and J. Lanjouw, eds.), Vol.2. pp. 1-267.

Scott, H.J.,Jr., Struhsaker, T.T., Glander, K. and Chirivi, H. (1976). Primates and their habitats in northern Colombia, with recommendations for future management and research. In: First Interamerican Conference on Conservation and Utilization of American Nonhuman Primates in Biomedical Research, pp. 30-50, Pan American Health Organization, Washington, D.C.

Smith, C.C. (1975). The coevolution of plants and seed predators. In: Coevolution of Animals and Plants (Gilbert, L.E. and P.H. Raven, eds). University of Texas Press.

Smythe, N. (1970). Relationships between fruiting seasons and seed dispersal methods in a Neotropical forest. Amer. Natur. 104: 25-35.

Snow, B.K. (1970). A field study of the Bearded Bellbird in Trinidad. Ibis 112: 299-329.

Snow, D.W. (1971). Evolutionary aspects of fruit-eating by birds. Ibis 113: 194-202.

Snow, B.K. and Snow, D.W. (1971). The feeding ecology of tanagers and honeycreepers in Trinidad. Auk 88: 291-322.

Staaij, F. van der (1975). Jacht in Bigi Poika. Mimeographed Report, Landbouwhogeschool Wageningen, Celos, Paramaribo, Suriname.

Struhsaker, T.T., Glander, K., Chirivi, H. and Scott, N.J. (1975). A survey of primates and their habitats in northern Colombia. In: Primate Censusing Studies in Peru and Colombia, pp. 43-78, Pan American Health Organisation.

Sugiyama, Y. (1973). The social structure of wild chimpanzees: a review of field studies. In: Comparative Ecology and Behaviour of Primates (R.P. Michael and J.H. Crook, eds.). Academic Press, London and New York.

Sugiyama, Y. and Koman, J. (1979). Social structure and dynamics of wild chimpanzees at Bossou, Guinea. Primates 20: 323-339.

Tokuda, K. (1968). Group size and vertical distribution of New World monkeys in the basin of the Rio Putumayo, the Upper Amazon. Proc. 8th Congr. Anthrop. Sci., Vol.1, Anthropology, pp. 260-261, Science Council of Japan, Ueno Park, Tokyo.

Tutin, C.E.G. (1978). Chimpanzee sexual behavior. Ph.D. thesis, Edinburgh University.

Tutin, C.E.G. (1979). Mating patterns and reproductive strategies in a community of wild chimpanzees (*Pan troglodytes schweinfurthii*). Behavioral Ecology and Sociobiology 6: 29-38.

Tutin, C.E.G. (1979).Responses of chimpanzees to copulation with special reference to interference by immature individuals. Anim. Behav. 27: 845-854.

Van der Pijl, L. (1969). Principles of dispersal in higher plants. Springer Verlag: New York.

Wagner, H.O. (1956). Freilandbeobachtungen an Klammeraffen. Z. Tierpsych. 13(2): 302-313.

Walsh, J. and Gannon, R. (1967). Time is short and the water rises. Thomas Nelson and Sons, London.

Wolf, R.H., Harrison, R.M. and Martin, T.W. (1975). A review of reproductive patterns in New World monkeys. Lab. Anim. Sci. 25(6): 814-821.

Wrangham, R.W. (1975). Behavioural ecology of chimpanzees in Gombe National Park, Tanzania. Ph.D. thesis, University of Cambridge.

Wrangham, R.W. (1977). Feeding behaviour of chimpanzees in Gombe National Park, Tanzania. In: Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes (T.H. Clutton-Brock, ed.) Academic Press, London.

Wrangham, R.W. (1979). On the evolution of ape social system. Social Science Information 18: 335-368.

ADDITIONAL REFERENCES

Alvarez del Toro, M. (1977). Los Mamiferos de Chiapas. Universidad Autonoma de Chiapas, Tuxtla Gutierrez, Chiapas, Mexico.

Cant, J.G.H. (1977). Ecology, locomotion and social organization of spider monkeys (*Ateles geoffroyi*). Unpublished doctoral dissertation, Univ. of California, Davis.

Cant, J.G.H. (1979). Dispersal of *Stemmadenia donnell-smithii* by birds and monkeys. Biotropica 11: 122.

Davis, H. (1966). Field checklist of the birds of the Guianas. Florida Audubon Society.

Ellefson, J.O. (1974). A natural history of gibbons in the Malay Peninsula. In: Gibbon and Siamang (D. Rumbaugh, ed.), Vol. 3: 1-136. Karger, Basel.

Fleagle, J.G. (1976). Locomotion and posture of the Malayan siamang and implications for hominoid evolution. Folia primatol. 26: 245-269.

Goodall, J. (1965). Chimpanzees of the Gombe Stream Reserve. In: Primate Behavior (I. DeVore, ed.), 425-473. Holt, Rinehart and Winston, New York.

Goodman, L. and Wislocki, G.B. (1935). The cyclical uterine bleeding in a New World Monkey (*Ateles geoffroyi*). Anatomical Record 61: 379-387.

Groves, C.P. (1972). Phylogeny and classification of primates. In: Pathology of Simian Primates, Part 1 (R.N.T.-W. Fiennes, ed.), Karger, Basel.

Halperin, S.D. (1978). Grouping patterns of chimpanzees in Gombe National Park, Tanzania. In: Perspectives on Human Evolution Vol. IV: The Behaviour of Great Apes (D.A. Hamburg and J. Goodall, eds). Staples (W.A. Benjamin, London and New York).

Hartley, P.H.T. (1935). An ecological study of the feeding habits of English titmice. J. Anim. Ecol. 22: 261-288.

Heltne, P.G., Freese, C. and Whitesides, G. (1975). A field survey of nonhuman primate populations in Bolivia. PanAmerican Health Organization.

Hladik, C.M. (1973). Alimentation et activité d'un groupe de Chimpanzés réintroduits en forêt gabonaise. La Terre et la Vie 27: 343-413.

Izawa, K., Kimura, K. and Nieto, A.S. (1979). Grouping of the wild spider monkey. Primates 20: 503-512.

Janson, C. (1975). Unpublished Senior Thesis, Princeton University.

Janzen, D.H. (1969). Seed-eaters versus seed size, number, toxicity and dispersal. Evolution 23: 1-27.

Janzen, D.H. (1971). Seed predation by animals. Ann. Rev. Ecol. Syst. 2: 465-492.

McKey, D. (1975). The ecology of coevolved seed dispersal systems. In: Coevolution of Animals and Plants (Gilbert, L.E. and P.H. Raven, eds). Univ. of Texas Press.

Mittermeier, R.A. (1973). Group activity and population dynamics of the howler monkey on Barro Colorado Island. Primates 14: 1-19.

Mittermeier, R.A. and Milton, K. (1976). Jungle jackpot. Animal Kingdom 79 (6): 26-32.

Mittermeier, R.A. (1978). Locomotion and posture in *Ateles geoffroyi* and *Ateles paniscus*. Folia primatol. 30: 161-193.

Morton, E.S. (1973). On the evolutionary advantages and disadvantages of fruit eating in tropical birds. Amer. Natur. 107: 8-22.

Moynihan, M. (1970). Some behavior patterns of platyrrhine monkeys. II. *Saguinus geoffroyi* and some other tamarins. Smithson. Contrib. Zool. 28: 1-77.

Nishida, T. (1974). Ecology of wild chimpanzees. In: Human Ecology (A. Ohtsuka, J. Tanaka and T. Nishida, eds). Kyoritsu-Shuppan, Tokyo.

Nishida, T. (1979). Population-specific habits among wild chimpanzees. Jinruigaku Zasshi/ J. anthrop. Soc. Nippon 87: 196-197.

Pusey, A.E. (1978). The physical and social development of wild adolescent chimpanzees (*Pan troglodytes schweinfurthii*). Diss. Abstr. Int. B38: 5791-5792.

Richards, P.W. (1952). The Tropical Rain Forest. Cambridge Univ. Press.

Sabater Pi, J. (1979). Feeding behaviour and diet of chimpanzees (*Pan troglodytes troglodytes*) in the Okorobiko Mountains of Rio Muni (West Africa). Zeitschrift für Tierpsychologie 50: 265-281.

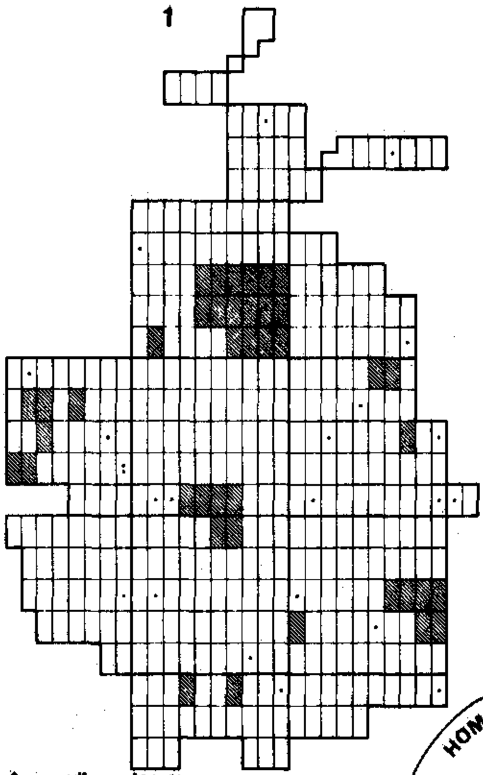
Appendix

Distribution and density of main food plant and sleeping tree species in the combined core area of two dominant-female spider monkeys belonging to the Voltzberg study group, of which ranging behaviour was best studied. For plotting purposes, the area was subdivided in rectangular ¼-hectare blocks. Shaded areas indicate non-suitable habitat (e.g., open granite, liane forest) that was not sampled. Both botanical and vernacular names (when available) are given, while the total number of individual plants plotted in the area is given in parentheses. Few species (no. 53 and 119) were very abundant locally and consequently only part of its population was plotted. Of several species, in particular lianes, only the individual plants actually seen exploited by the monkeys were plotted (no. 25,26,27, 93,115 and 116). For the purposes of this study, tagging and plotting was restricted to those individual plants, that obviously had reached 'their' preferred stratum which, in general, implies the phenomenon of flowering and fruiting. Plants providing the monkeys only with edible flush leaves were plotted when reaching at least 12 meters in height, the lower limit of *Ateles* vertical range.

Besides mountain savanna forest with indicator species *Guettarda acreana* (114) and *Ecclinusa guianensis* (119), pina swamp forest with indicator species *Euterpe oleracea*, *Bombax spectabile* (14), *Eperua falcata* (61) and *Virola surinamensis* (111), and high forest, a subtype of high forest on relatively red (ferrosiallitic) forest-soil may be distinguished, covering roughly blocks A and B, showing relatively abundant leading species like *Protium polybotryum* (18), *Tetragastris altissima* (19), *Tetragastris panamensis* (20) and *Capparis maroniensis* (21).

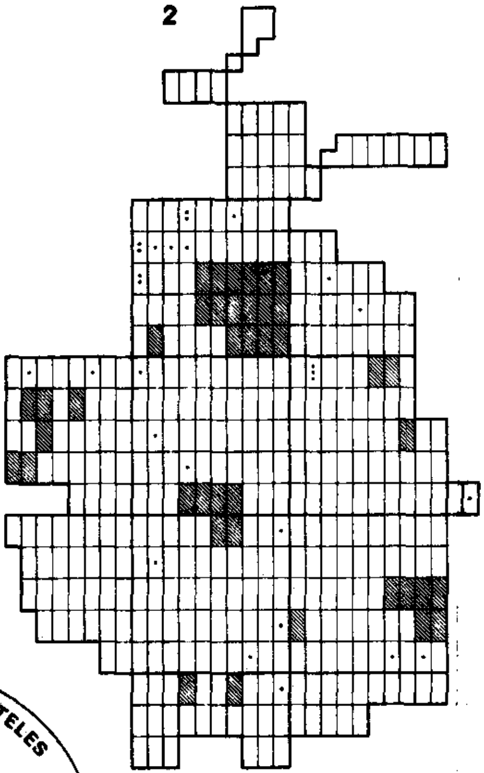
HOME RANGE SHOWING DISTRIBUTION AND DENSITY OF FOOD PLANTS

1

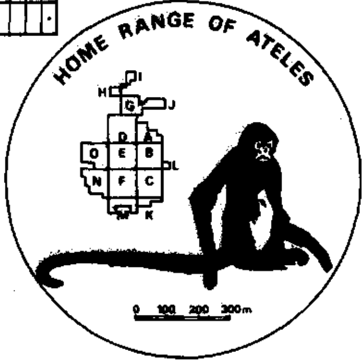


Anacardium giganteum
'boskasjoe'
(23)

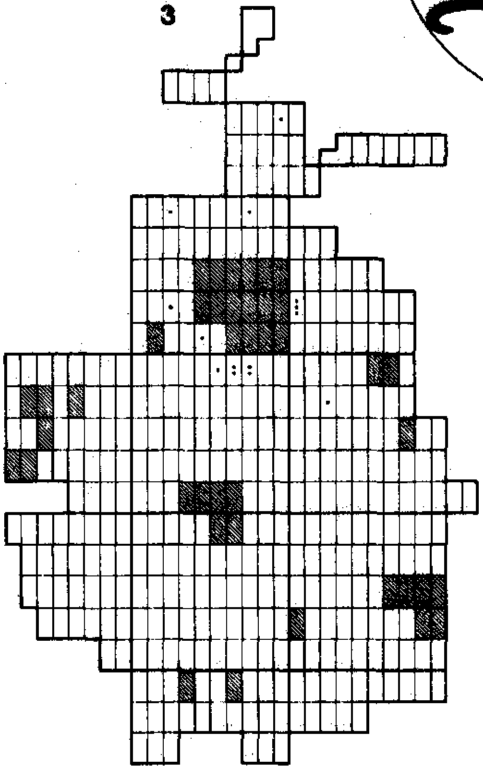
2



Spondias mombin
'mope'
(28)

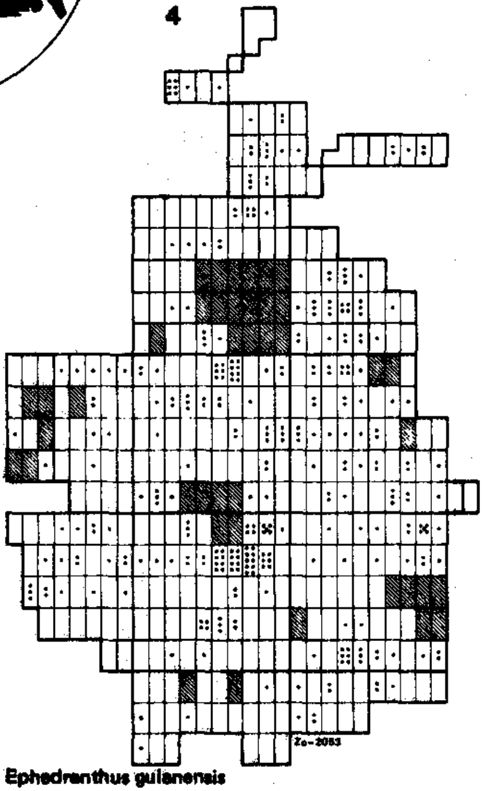


3



Duguetia sp.
'gele bast jari jari'
(14)

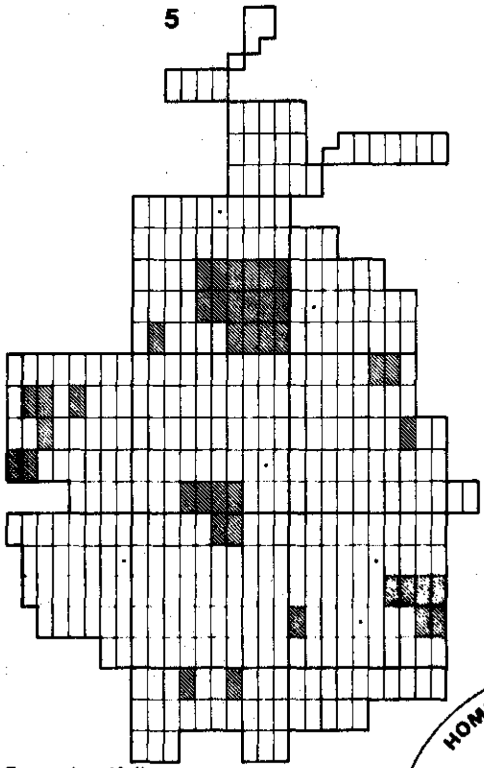
4



Ephedranthus guianensis
'man-pikapika'
(312)

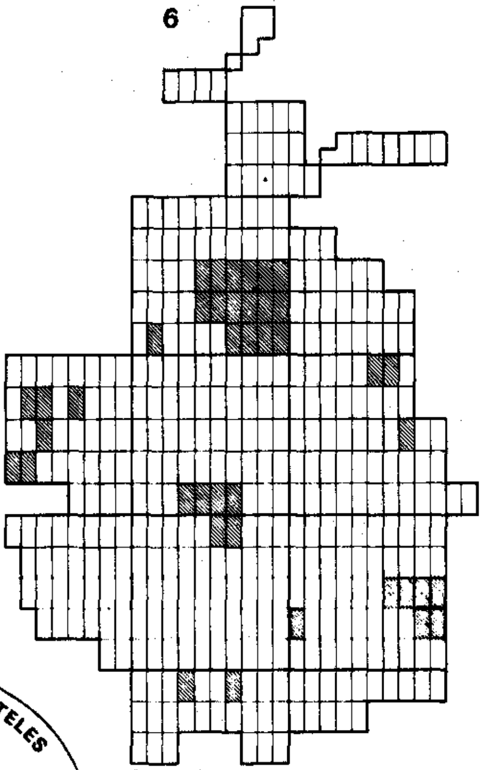
HOME RANGE SHOWING DISTRIBUTION AND DENSITY OF FOOD PLANTS

5

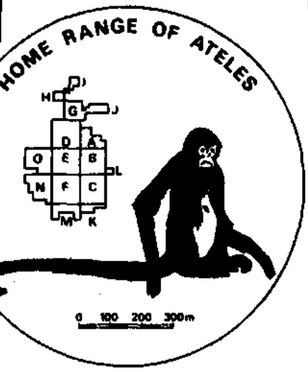


Fusaea longifolia
'langbladige jari jari'
(6)

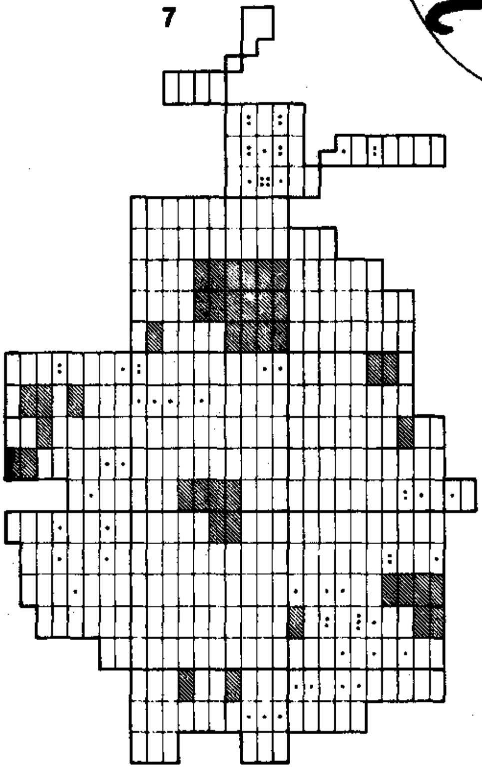
6



Guatteria chrysopetala
(1)

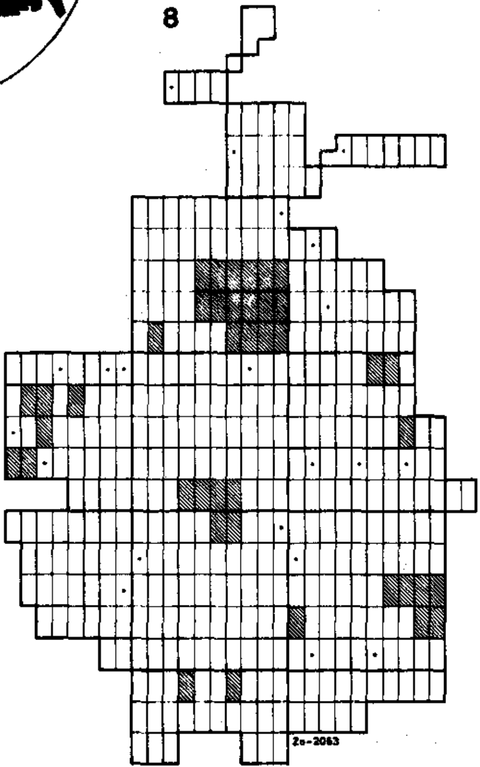


7



Unonopsis glaucopetala
'gewone jari jari'
(63)

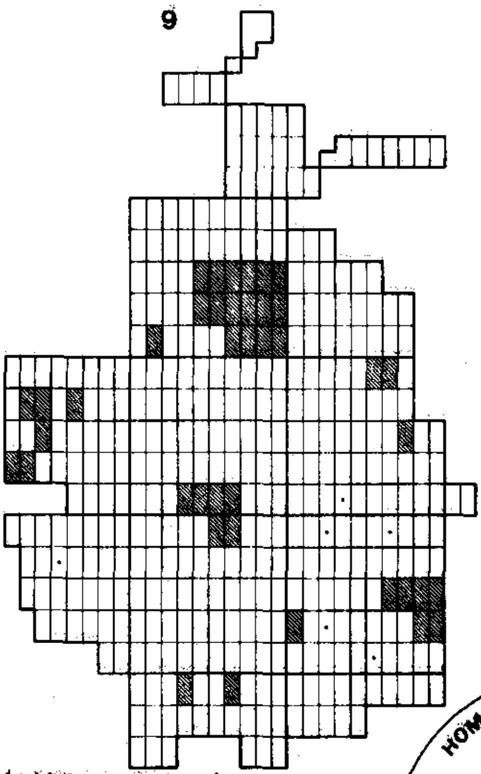
8



Aspidosperma excelsum
'zwart parelhout'
(21)

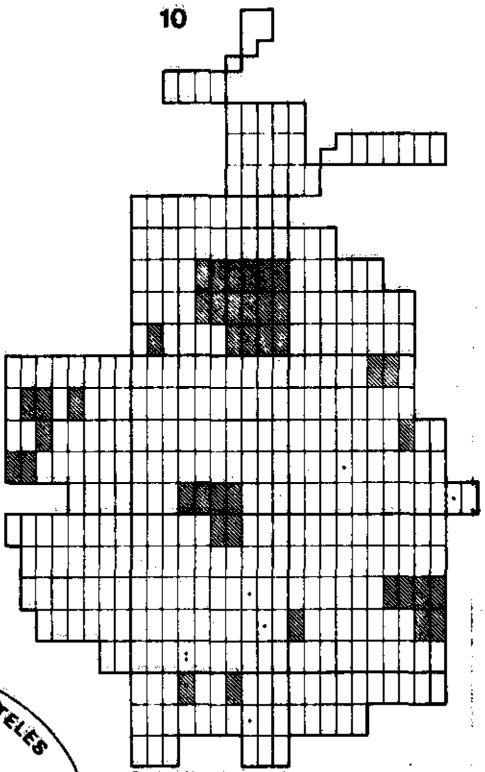
HOME RANGE SHOWING DISTRIBUTION AND DENSITY OF FOOD PLANTS

9

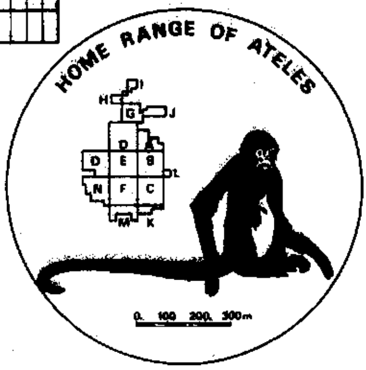


Aspidosperma marcgravianum
'wit parelhout'
(6)

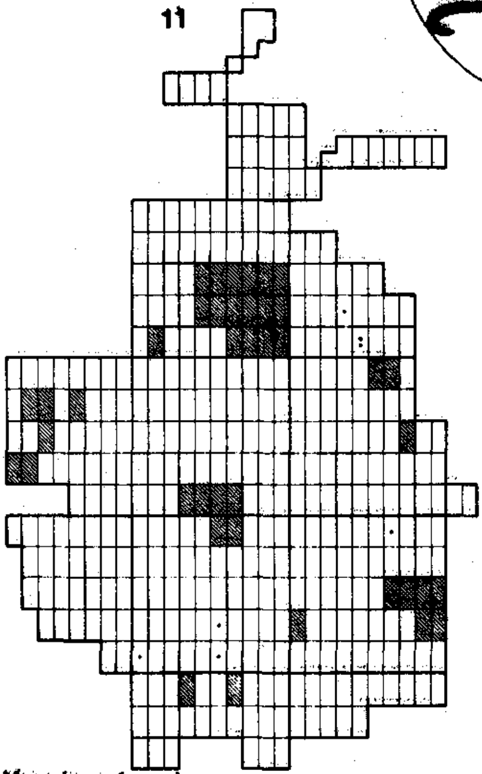
10



Geissospermum sp.
'hoogland bergi-bita'
(7)

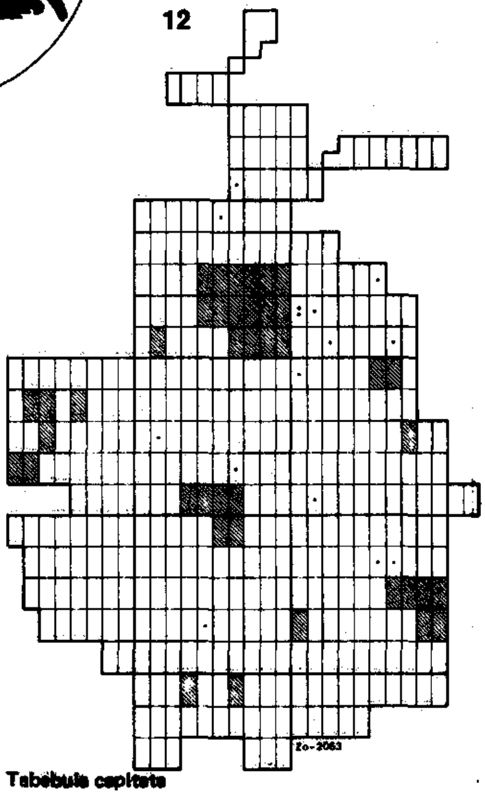


11



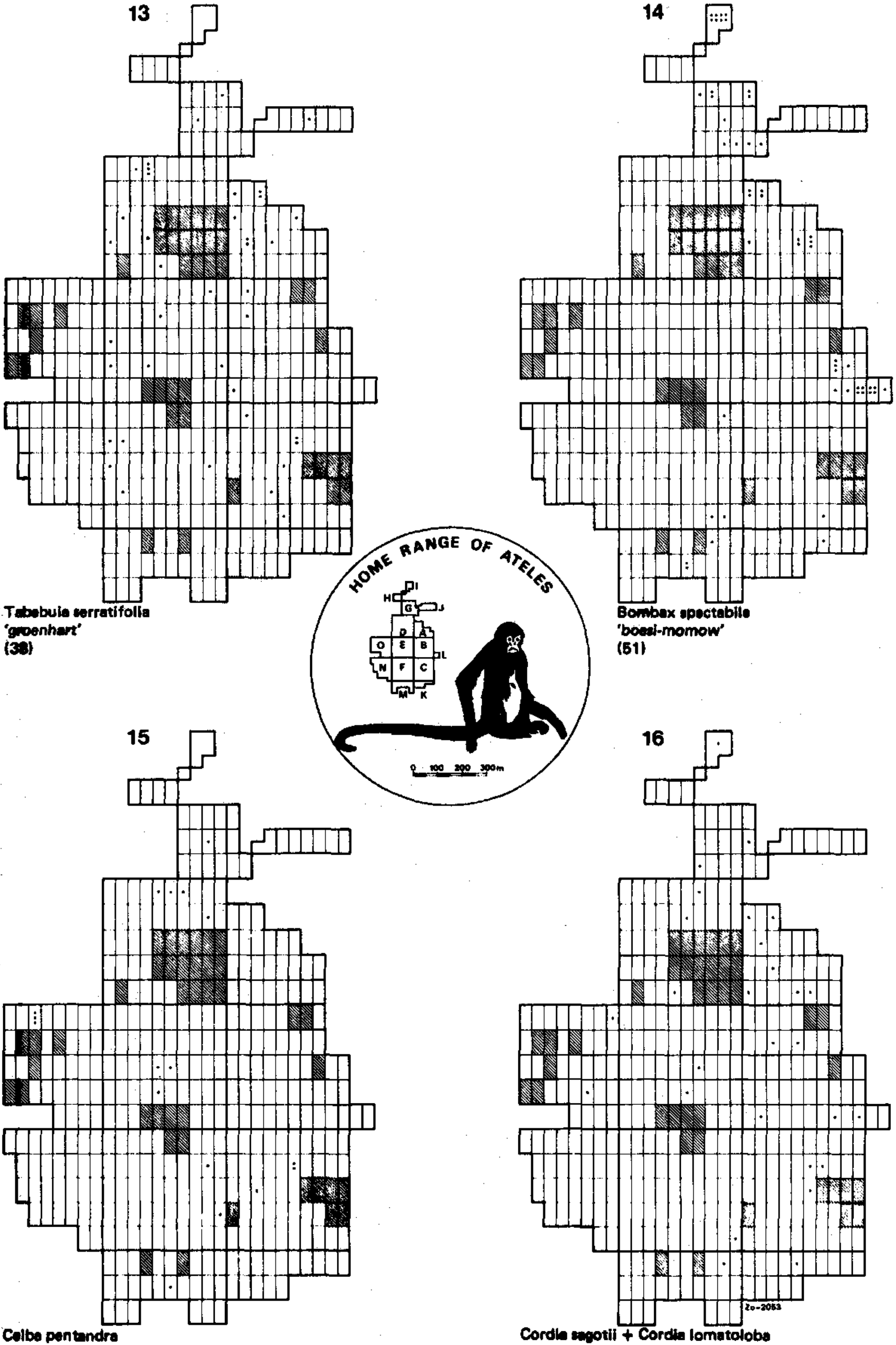
Macoubea guianensis
'sokosoko-mapa'
(7)

12



Tabebuia capitata
'makagrin'
(15)

HOME RANGE SHOWING DISTRIBUTION AND DENSITY OF FOOD PLANTS



Tabebuia serratifolia
'groenhart'
(38)

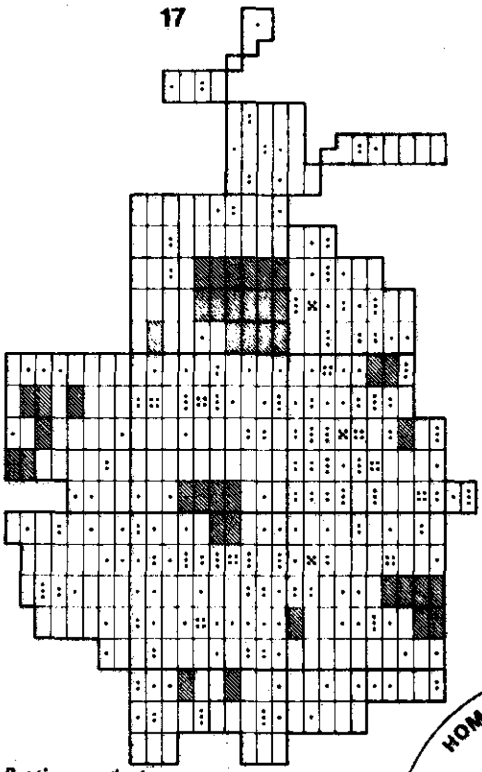
Bombax spectabile
'bossi-momow'
(51)

Ceiba pentandra
'kankantri'
(18)

Cordia sagotii + Cordia lomatoloba
'hoogland tafrabon'
(28)

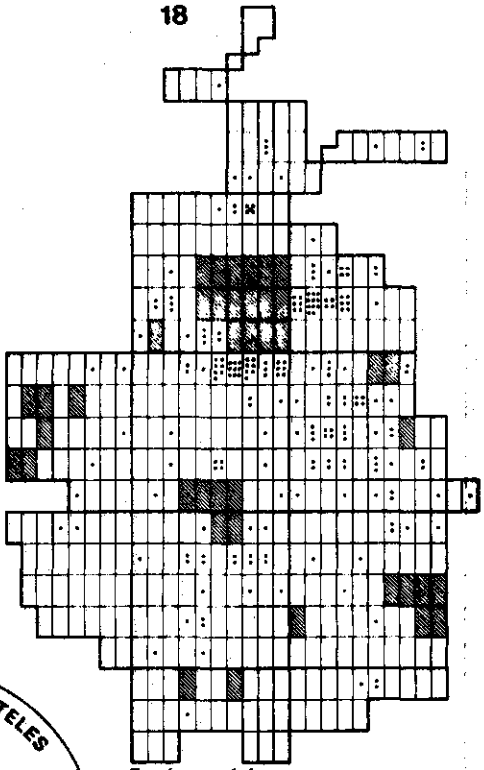
HOME RANGE SHOWING DISTRIBUTION AND DENSITY OF FOOD PLANTS

17

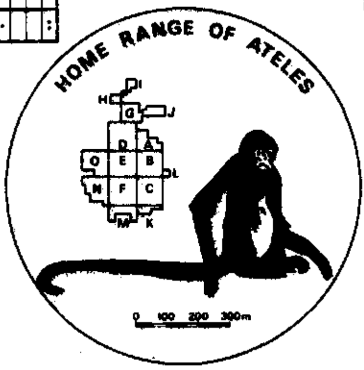


Protium neglectum
'grootbladige tingimoni'
(311)

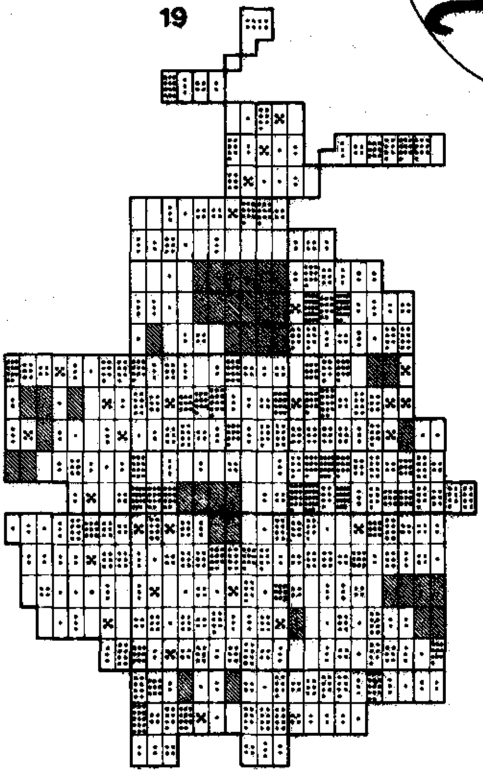
18



Protium polybotryum
'rode bast tingimoni'
(217)

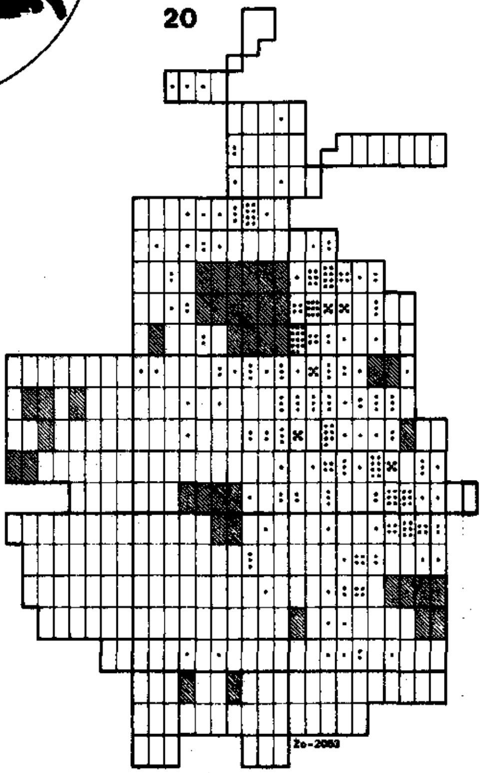


19



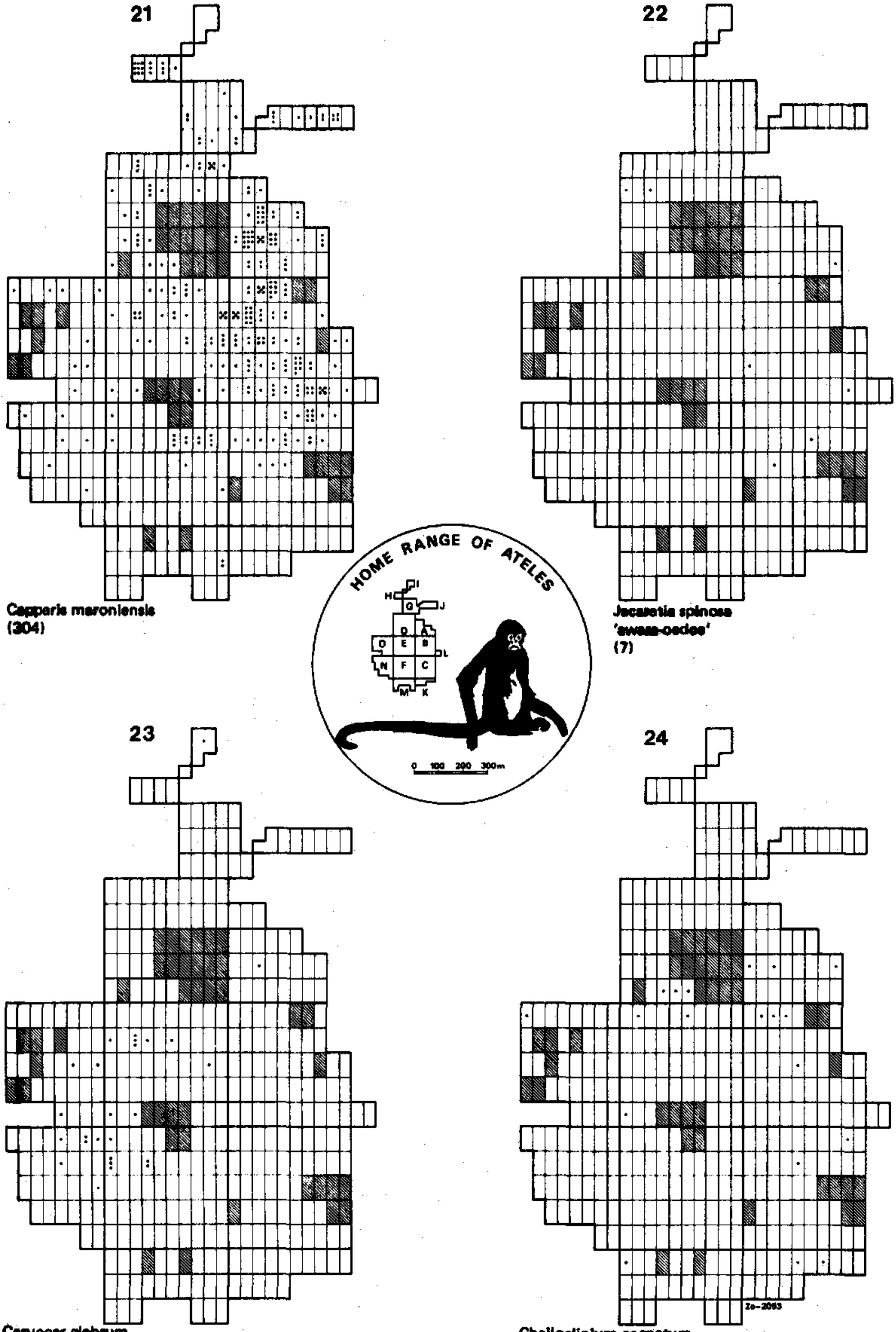
Tetragastris altissima
'rode sali'
(1631)

20



Tetragastris panamensis
'tingimoni-sali'
(280)

HOME RANGE SHOWING DISTRIBUTION AND DENSITY OF FOOD PLANTS



21

Capparis maroniensis
(304)

22

Jacaratia spinosa
'awasa-oedoe'
(7)

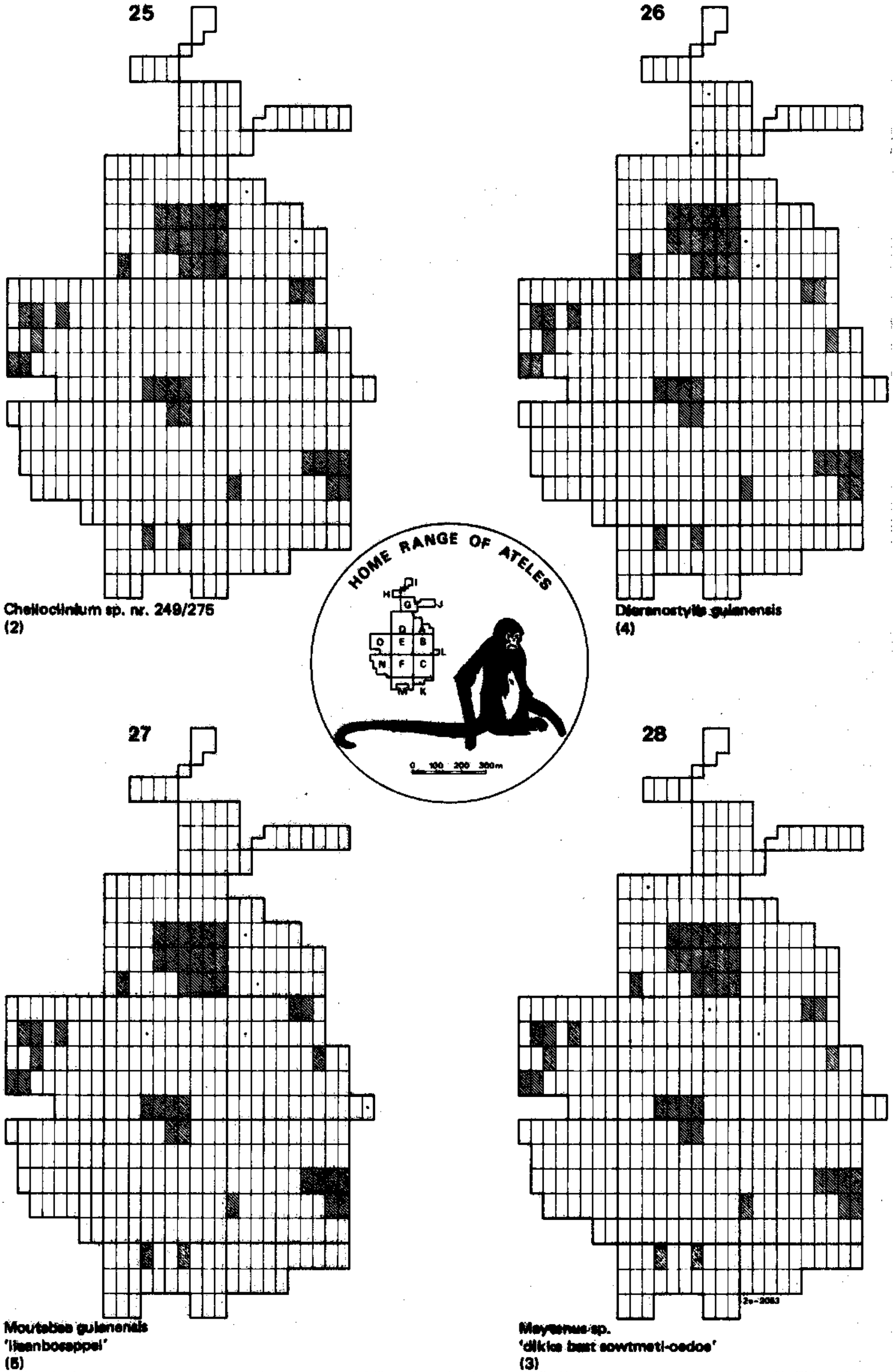
23

Caryocar glabrum
'gladde sopo-oedoe'
(28)

24

Cheiloclinium cognatum
'lisansowtmeti-oedoe'
(20)

HOME RANGE SHOWING DISTRIBUTION AND DENSITY OF FOOD PLANTS



Cheilocl inium sp. nr. 249/275
(2)

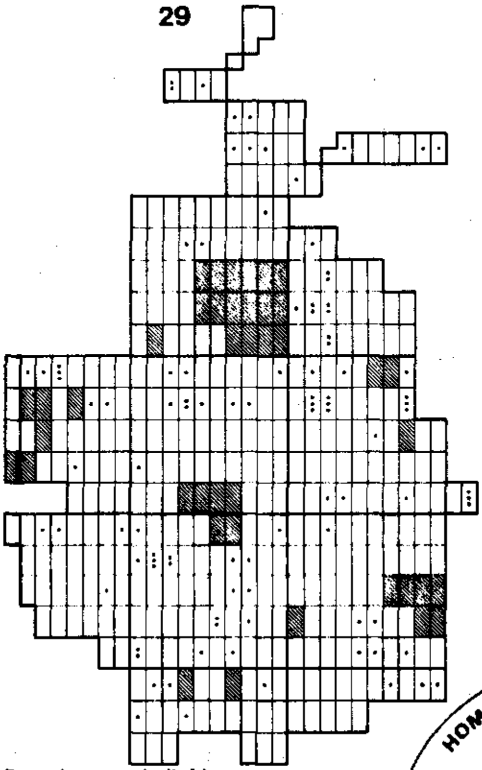
Dicranostylis guianensis
(4)

Moutabea guianensis
'lianboseppel'
(5)

Maytenus sp.
'dikkie bast sowtmeti-oedoe'
(3)

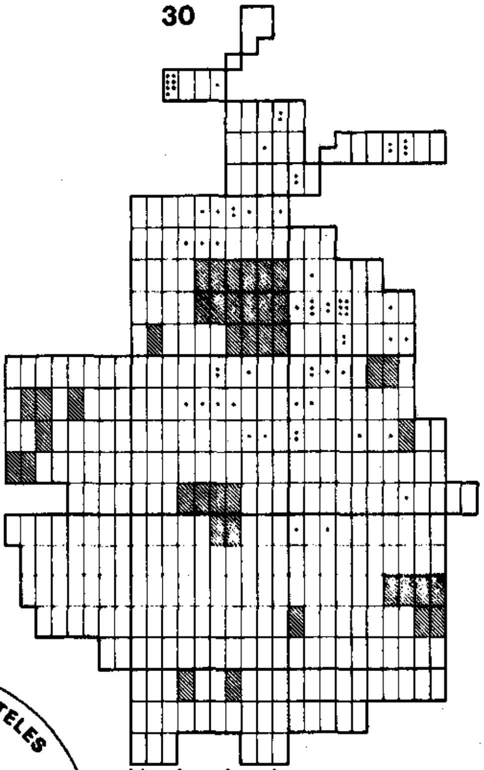
HOME RANGE SHOWING DISTRIBUTION AND DENSITY OF FOOD PLANTS

29

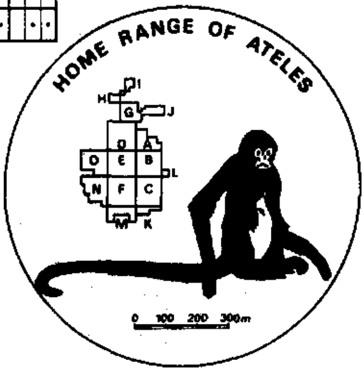


Couepia caryophylloides
'hoogland anawra'
(99)

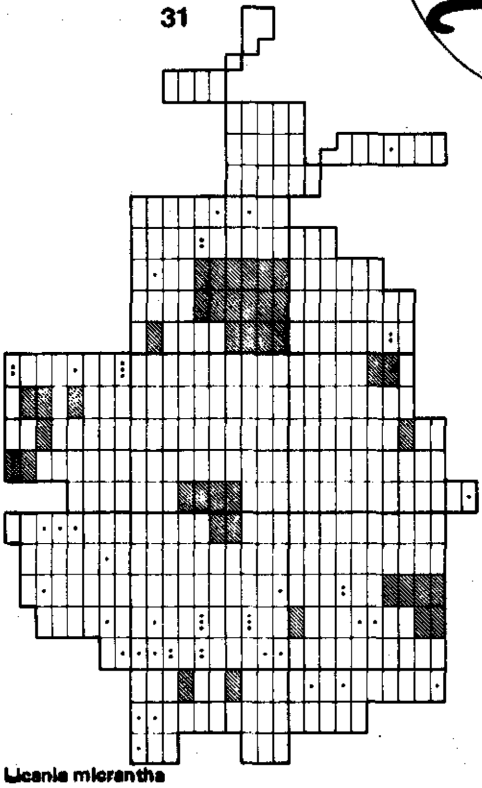
30



Licania majuscula
'harde bast kwepi'
(67)

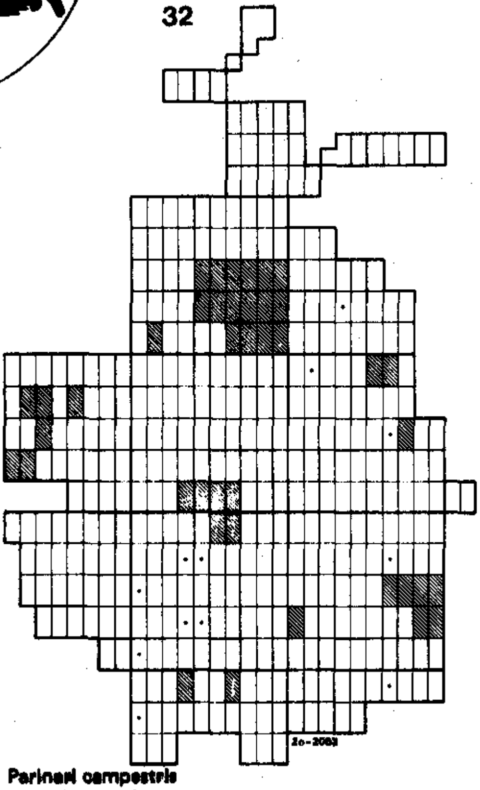


31



Licania micrantha
'swarte foengoe'
(49)

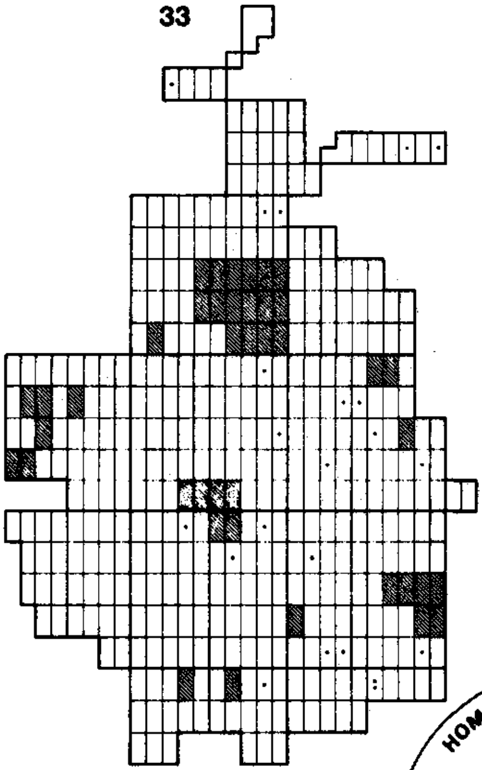
32



Parinari campestris
'rode foengoe'
(12)

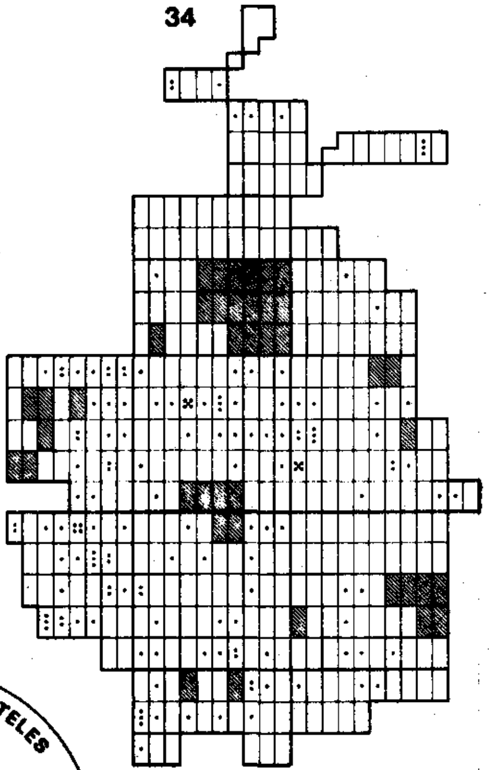
HOME RANGE SHOWING DISTRIBUTION AND DENSITY OF FOOD PLANTS

33

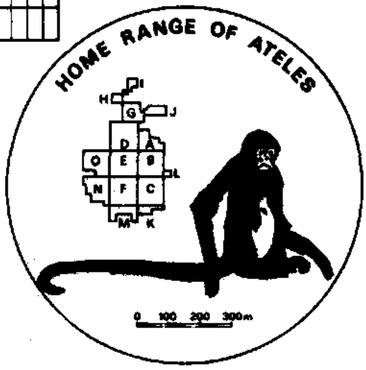


Parinari excelsa
'kleinbladige rode foengoe'
(22)

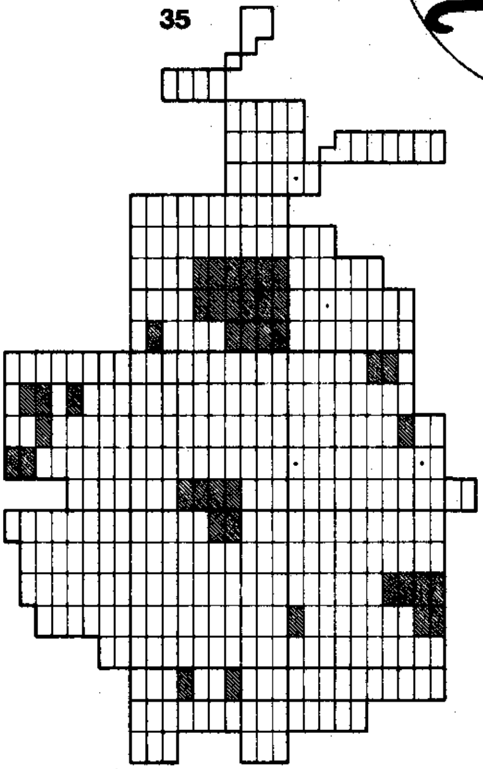
34



Buchenavia capitata
'djindja'-oedoe'
(150)

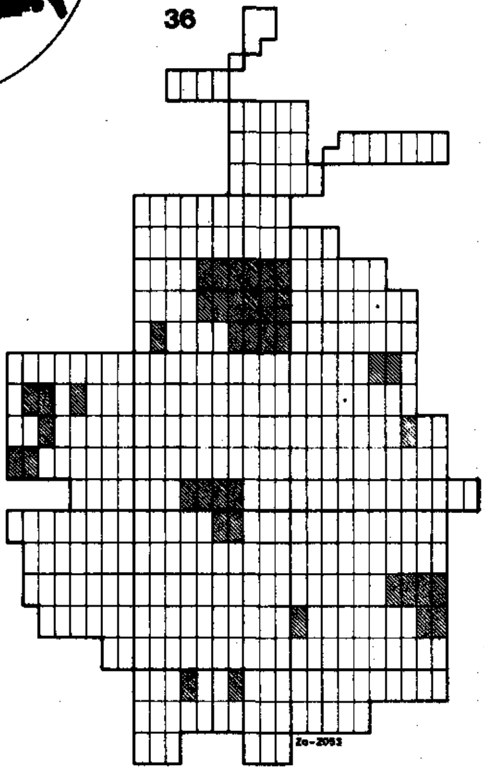


35



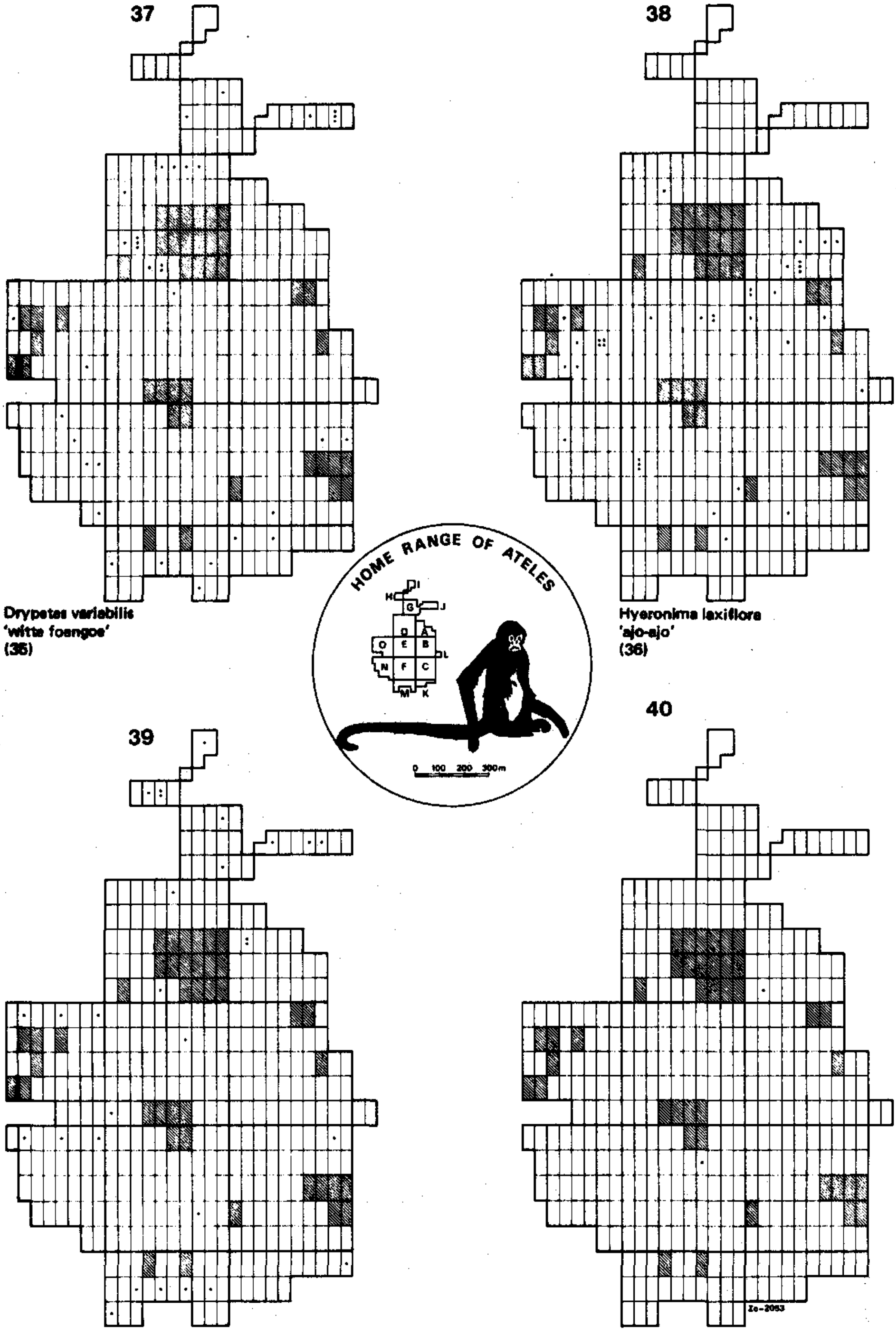
Maripa scandens
(4)

36



Alchorneopsis floribunda
'menbebe'
(2)

HOME RANGE SHOWING DISTRIBUTION AND DENSITY OF FOOD PLANTS



37

Drypetes variabilis
'witte foengoe'
(35)

38

Hyeronima laxiflora
'ajo-ajo'
(36)

39

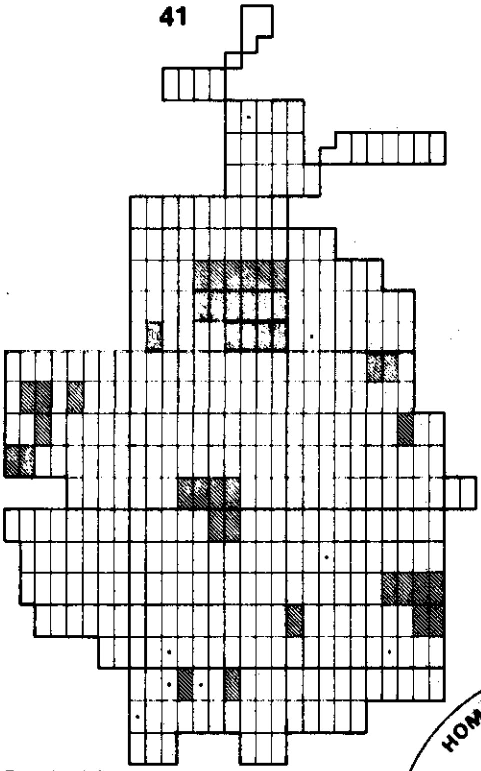
Laetia procera
'kaiman-oedoe/pintokopi'
(30)

40

Gnetum urens
(2)

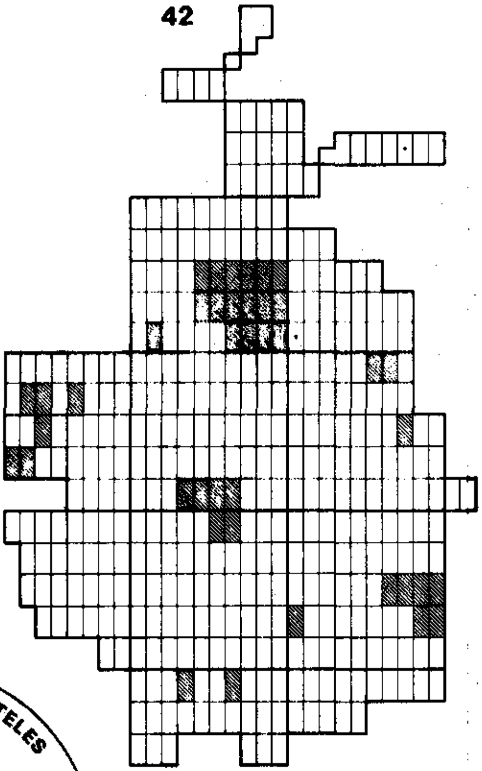
HOME RANGE SHOWING DISTRIBUTION AND DENSITY OF FOOD PLANTS

41

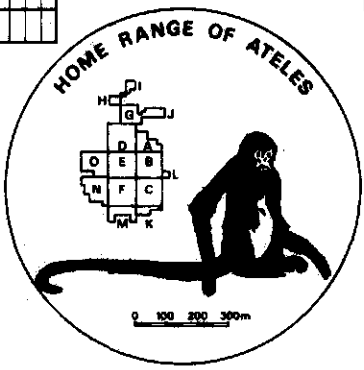


Goupia glabra
'kopi'
(8)

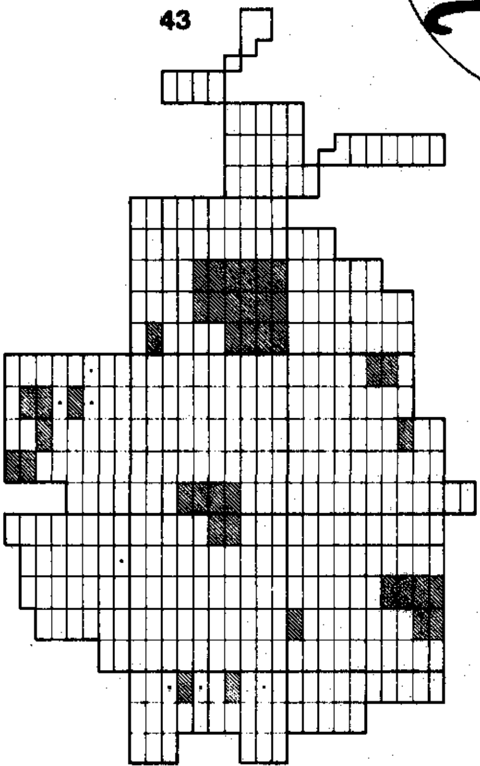
42



Platonia insignis
'geelhart/pakoeli'
(2)

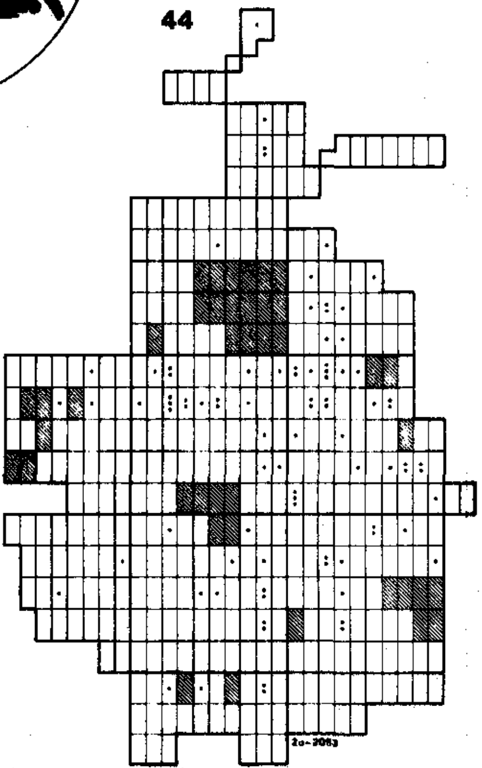


43



Rheedia benthamiana
'hoogland pakoeli'
(7)

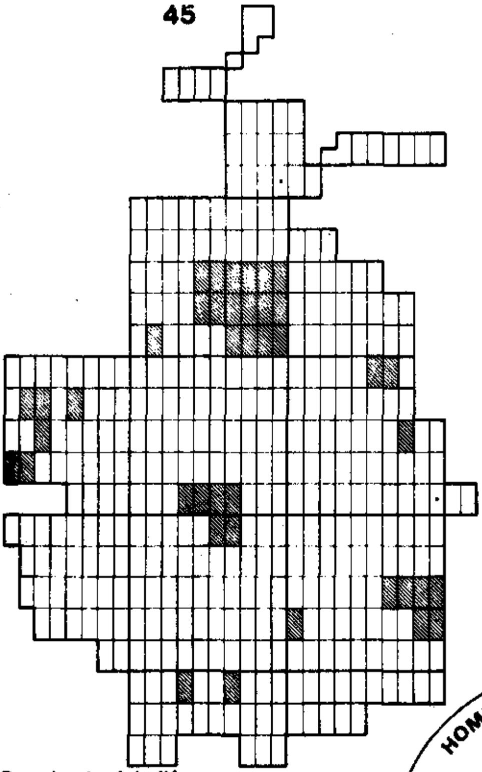
44



Rheedia macrophylla
'pakoeli'
(88)

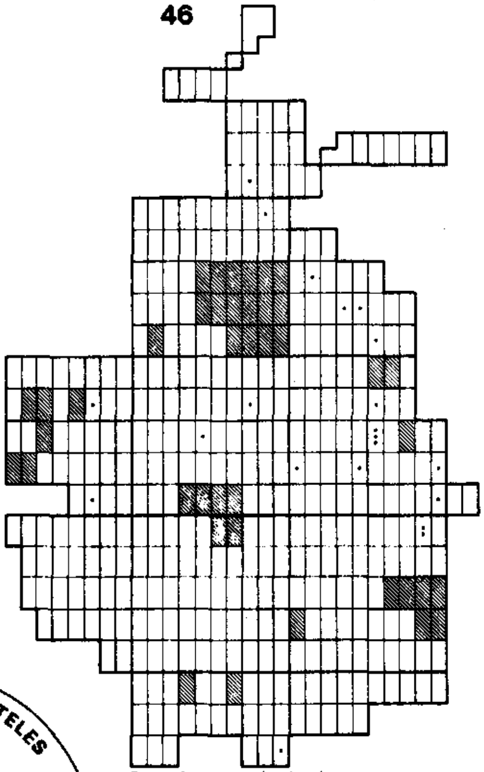
HOME RANGE SHOWING DISTRIBUTION AND DENSITY OF FOOD PLANTS

45

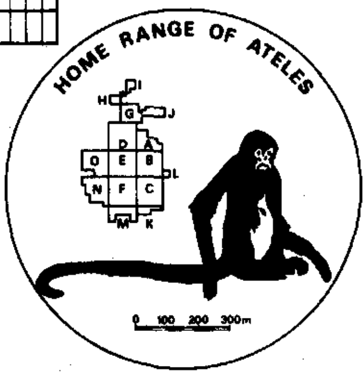


Symphonia globulifera
'mataki'
(2)

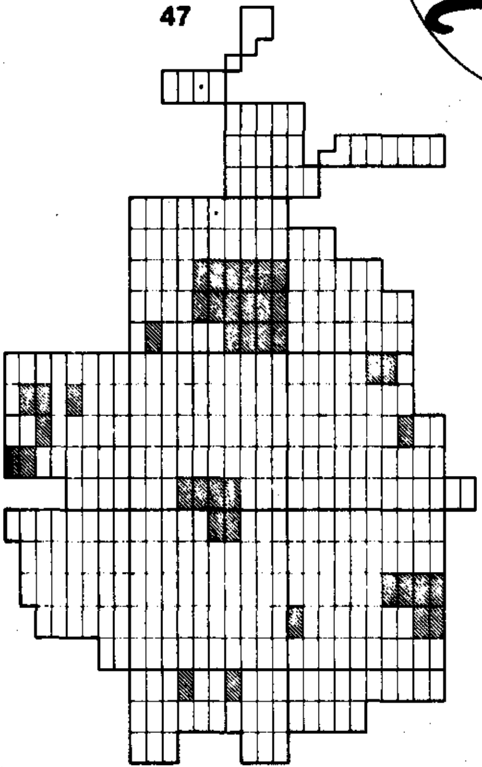
46



Sacoglottis cydonioides
'witte bast bofroe-oedoe'
(21)

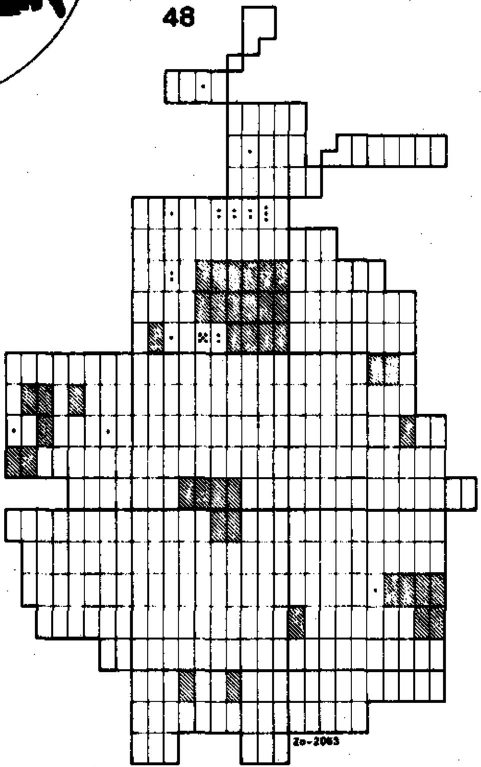


47



Licaria cayennensis
'kaneelhart'
(2)

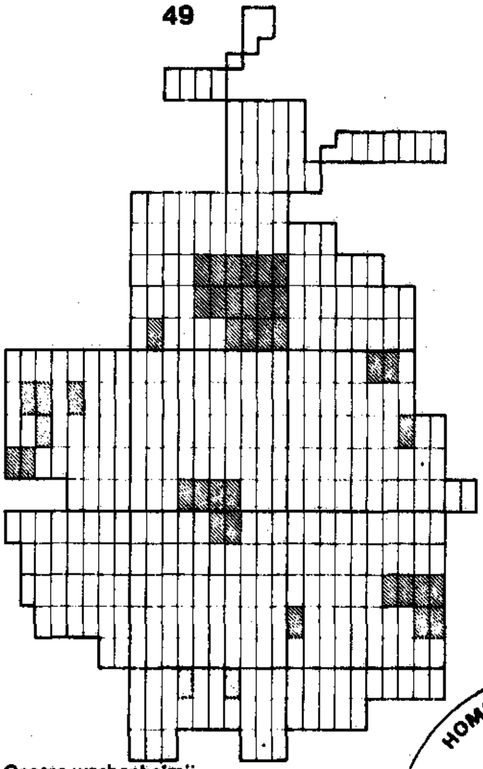
48



Nectandra cf. kunthiana
'grootbladige zwarte pisi'
(24)

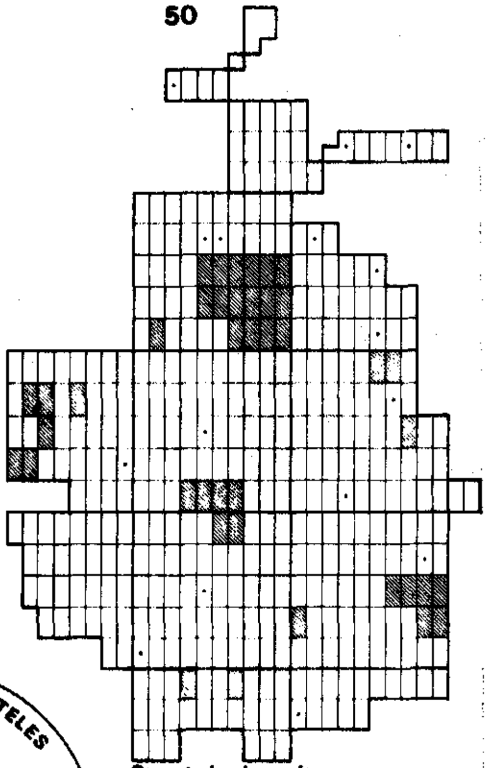
HOME RANGE SHOWING DISTRIBUTION AND DENSITY OF FOOD PLANTS

49

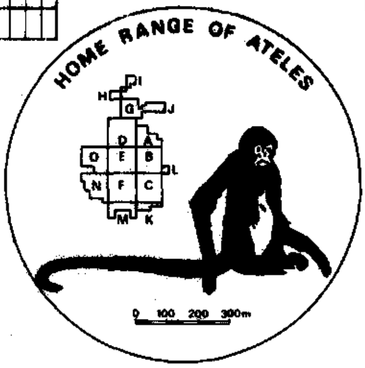


Ocotea wachenheimii
'pisi'
(2)

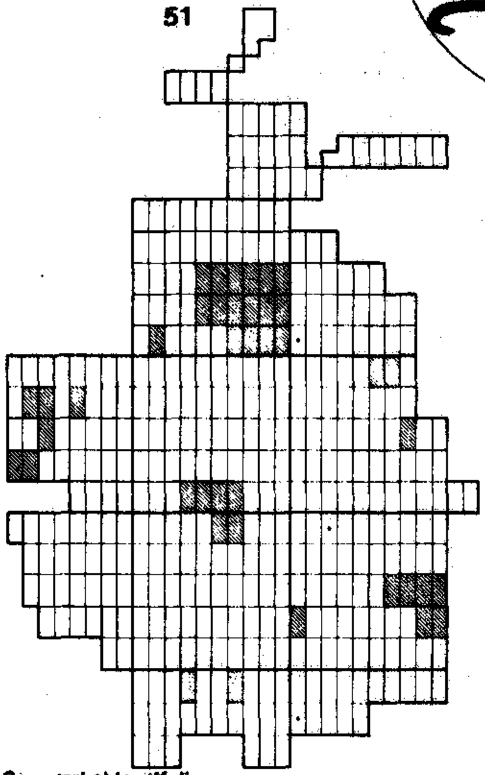
50



Couratari guianensis
'ingi-pipa'
(17)

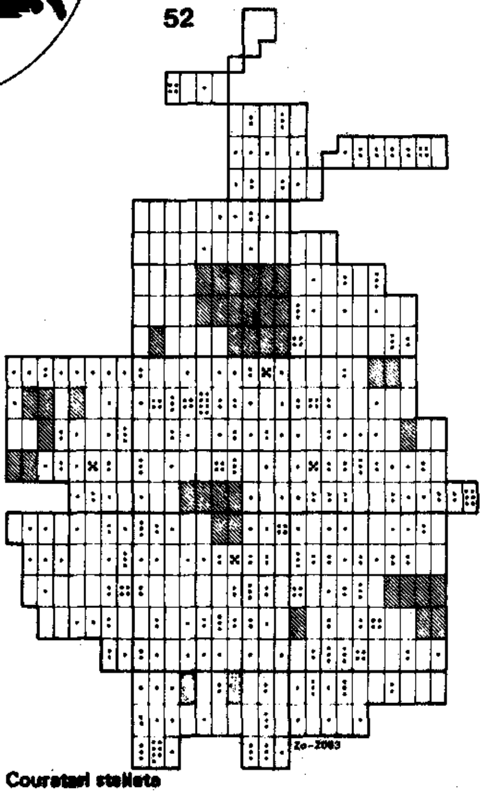


51



Couratari oblongifolia
'ingi-pipa'
(3)

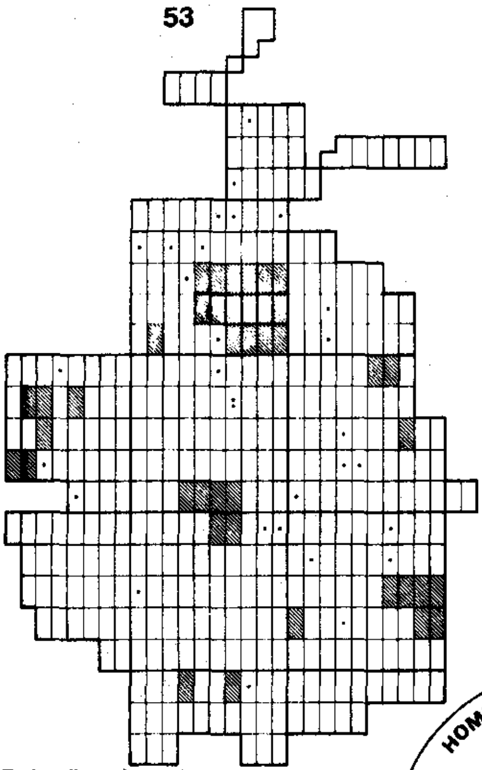
52



Couratari stellata
'ingi-pipa'
(403)

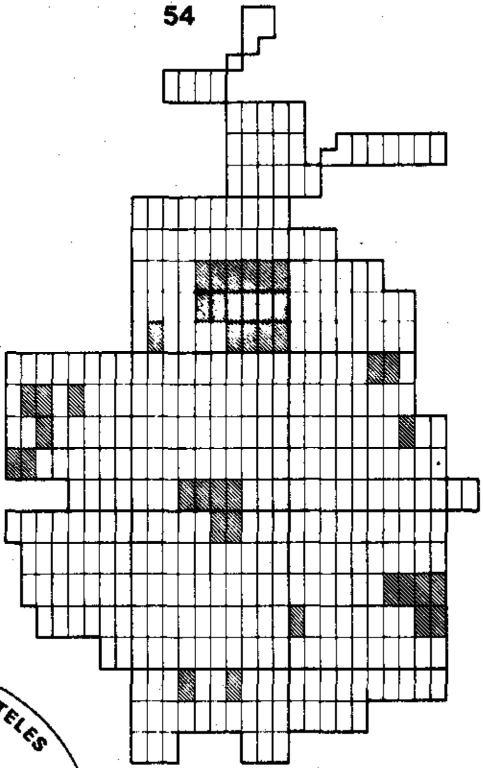
HOME RANGE: SHOWING DISTRIBUTION AND DENSITY OF FOOD PLANTS

53

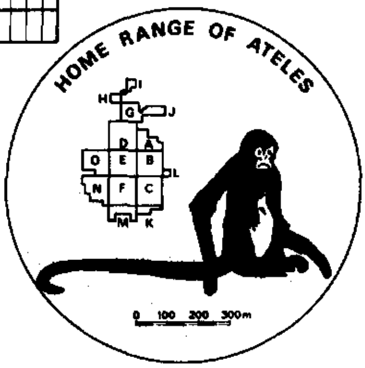


Eschweilera chartacea
'witte bast tité-oedoe'
(32)

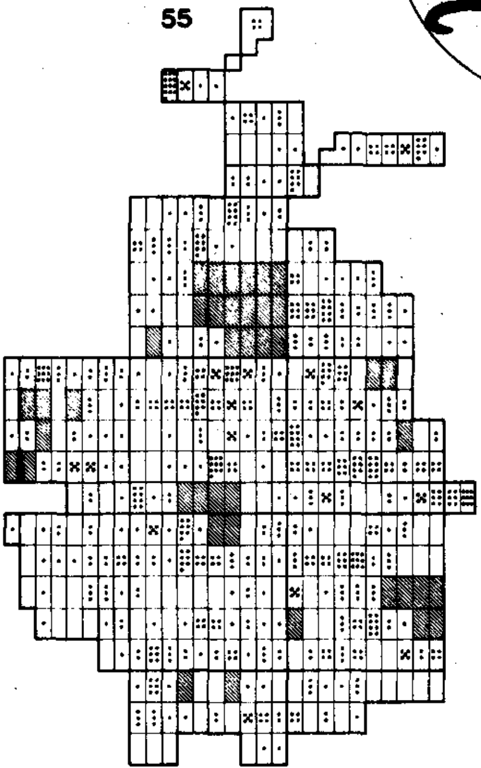
54



Eschweilera congestiflora
'oema-barklak'
(2)

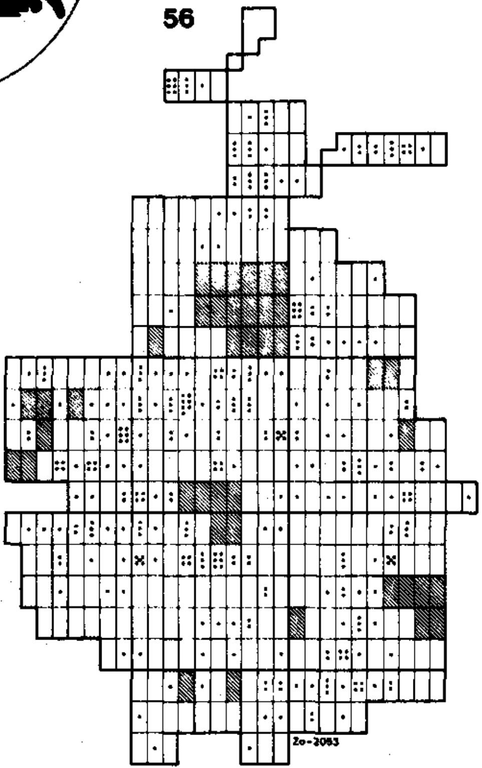


55



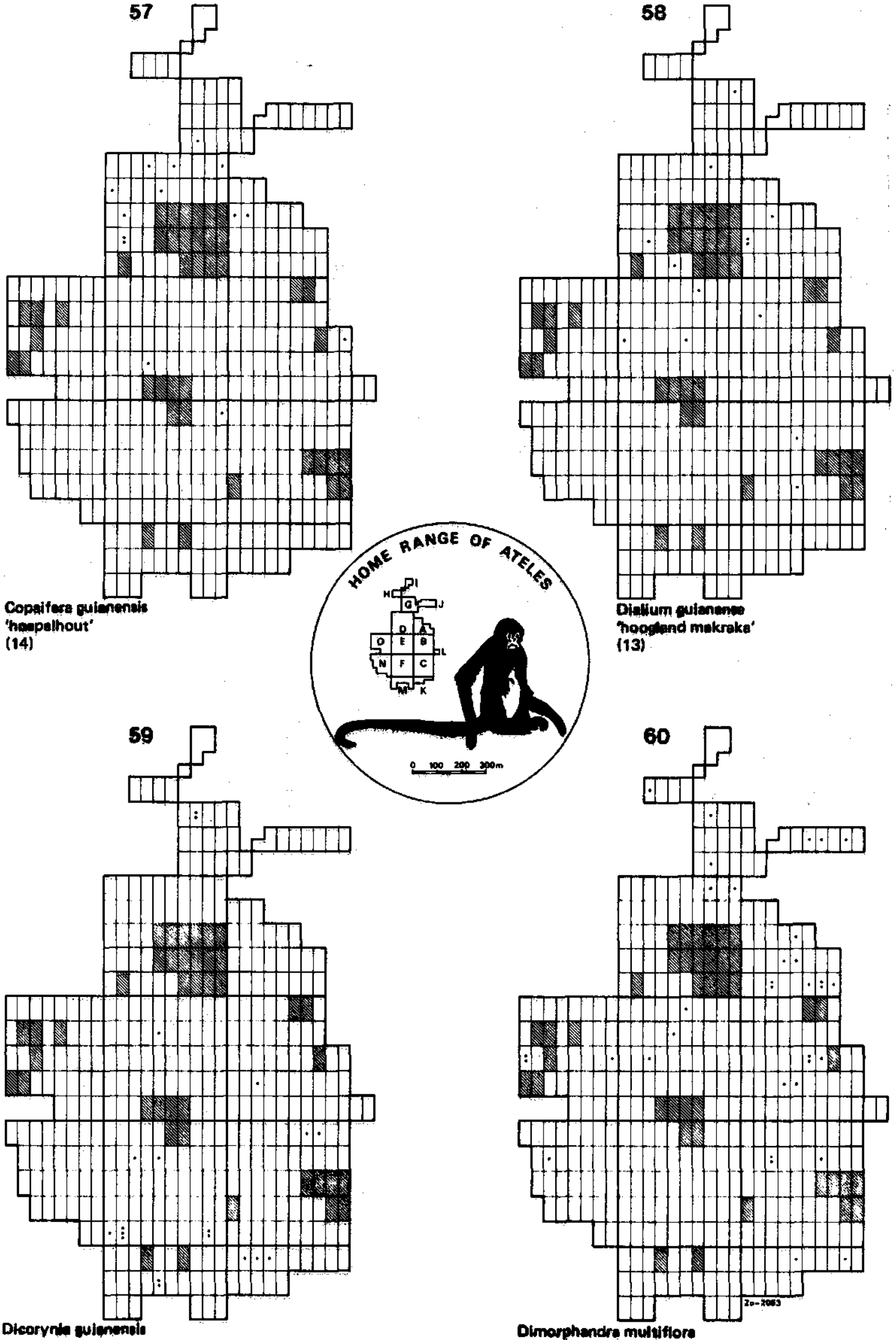
Eschweilera corrugata
'hoogland oema-barklak'
(761)

56



Eschweilera poiteaui
'gele bast tité-oedoe'
(336)

HOME RANGE SHOWING DISTRIBUTION AND DENSITY OF FOOD PLANTS



57: Copaifera guianensis 'hoepelhout' (14)

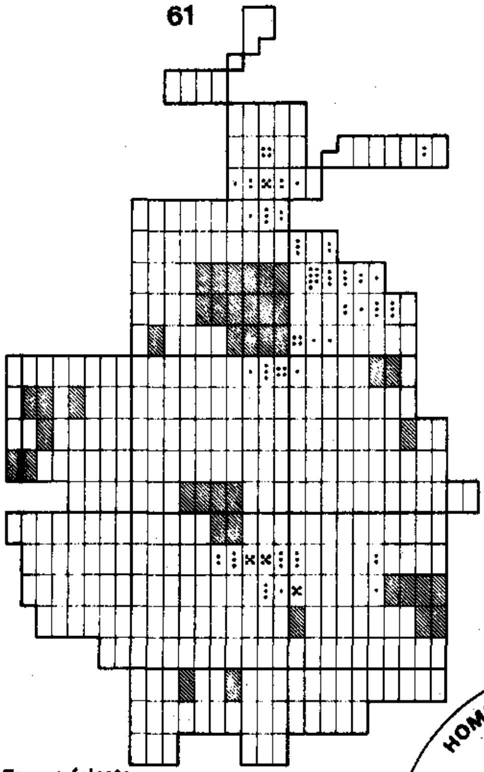
58: Dialium guianense 'hoogland makraka' (13)

59: Dicorynia guianensis 'basralokus' (19)

60: Dimorphandra multiflora (35)

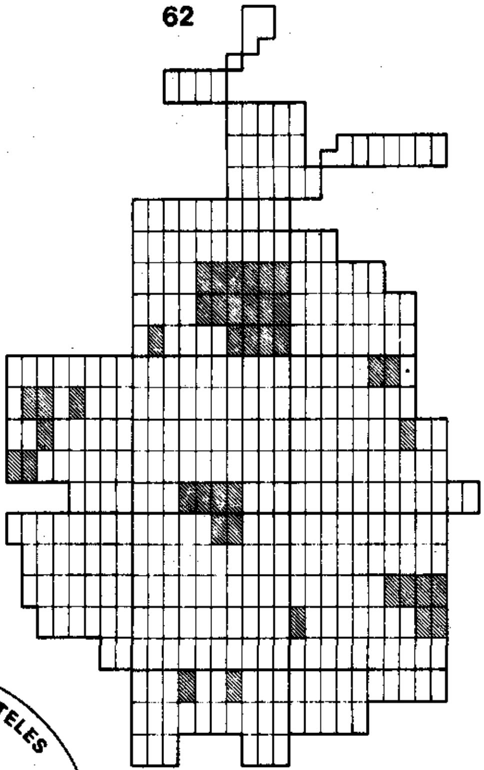
HOME RANGE SHOWING DISTRIBUTION AND DENSITY OF FOOD PLANTS

61

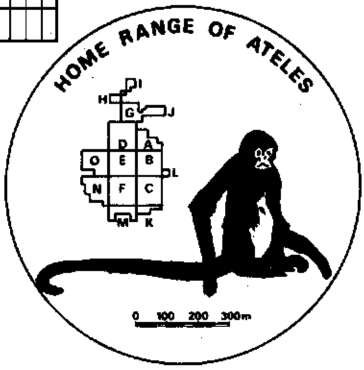


Eperua falcata
'walaba'
(102)

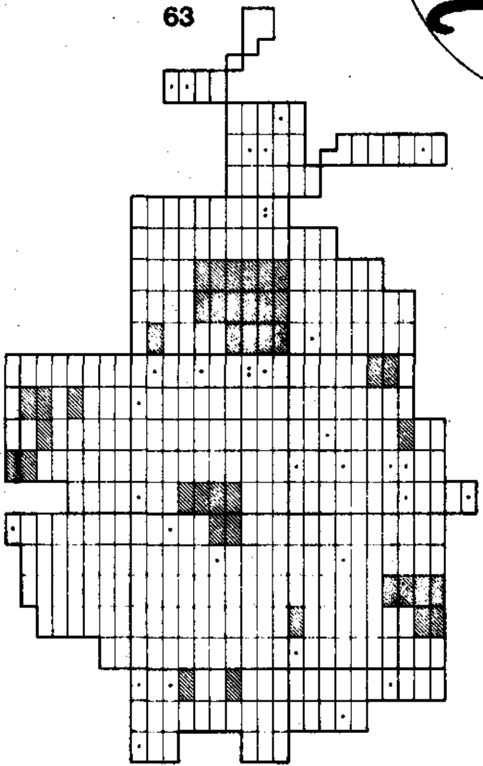
62



Eperua rubiginosa
'oeverwalaba'
(1)

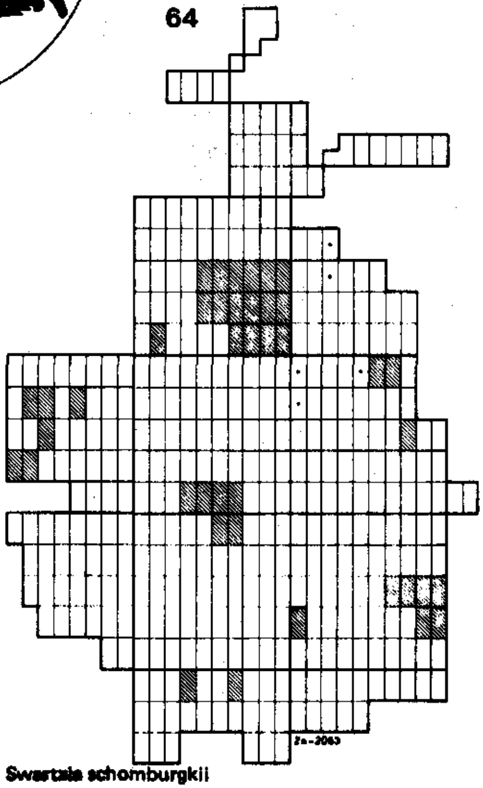


63



Swartzia remigifer
'witte boegoeboegoe'
(33)

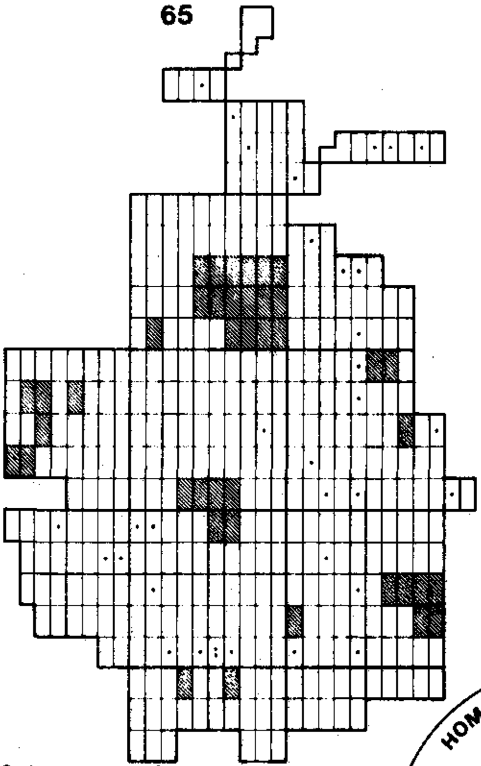
64



Swartzia schomburgkii
'zwarte boegoeboegoe'
(5)

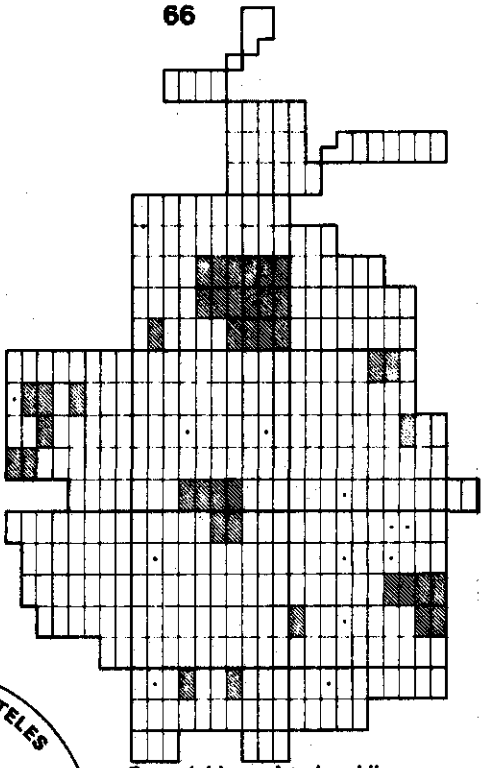
HOME RANGE SHOWING DISTRIBUTION AND DENSITY OF FOOD PLANTS

65

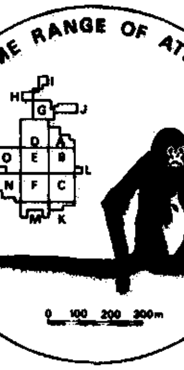


Cedrelinga cateniformis
'domceder'
(34)

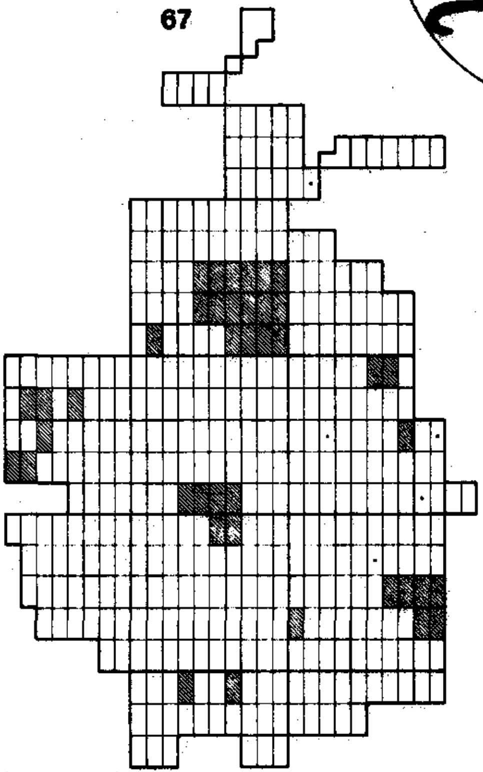
66



Enterolobium schomburgkii
'tamaren-prokoni'
(12)

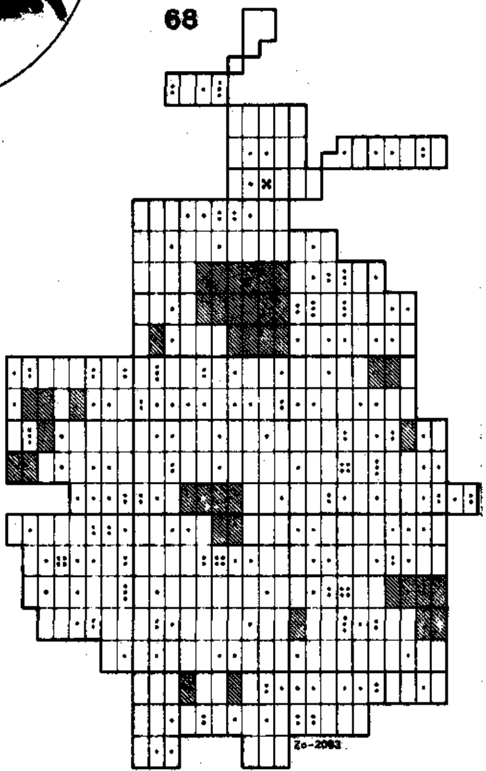


67



Inga acrocephala
'swit'bonki'
(6)

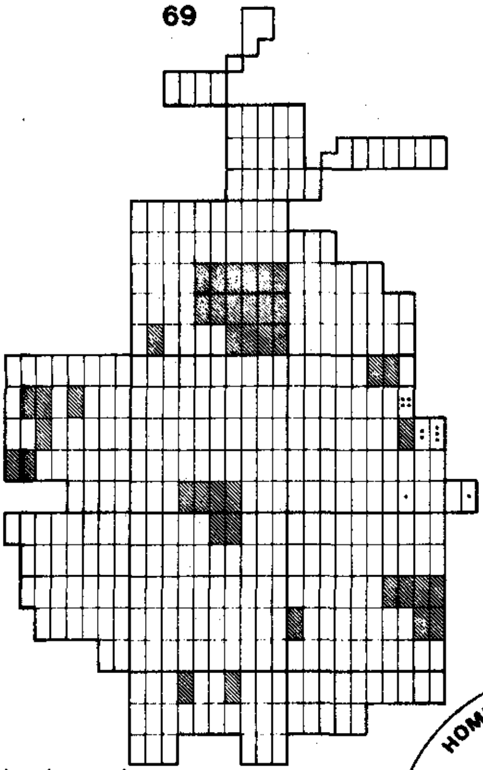
68



Inga alba
'rode prokoni'
(224)

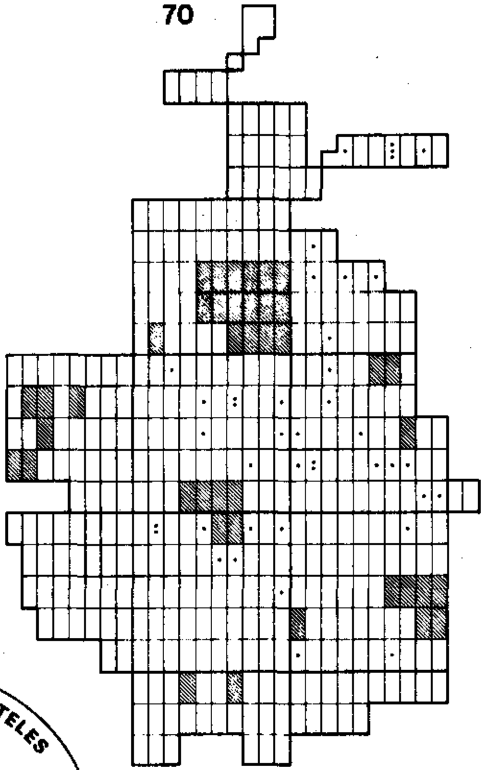
HOME RANGE SHOWING DISTRIBUTION AND DENSITY OF FOOD PLANTS

69

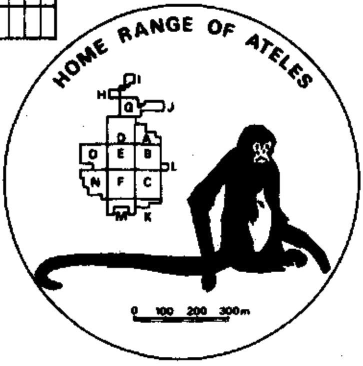


Inga bourgoni
'swit'bonki'
(11)

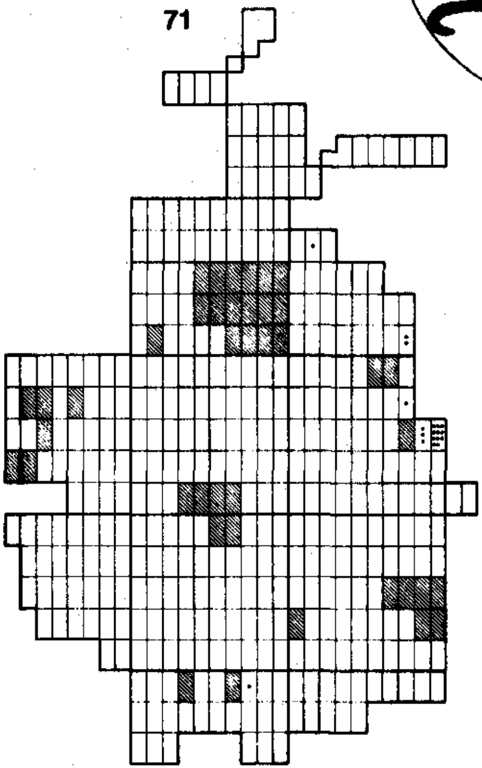
70



Inga cf. capitata
'swit'bonki'
(41)

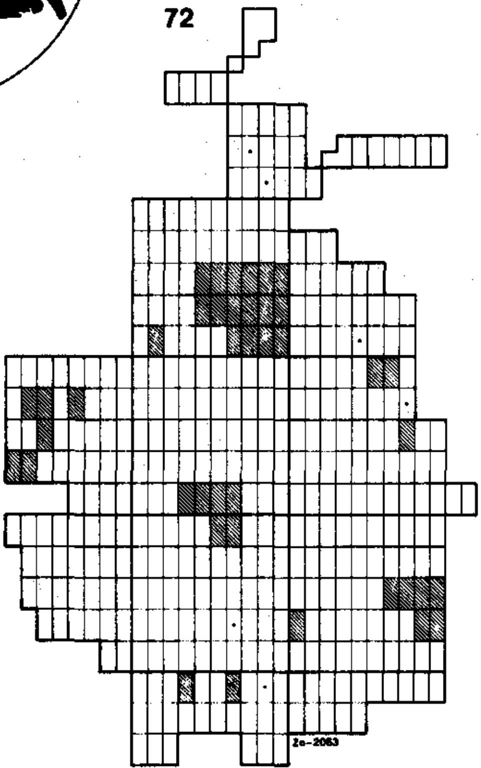


71



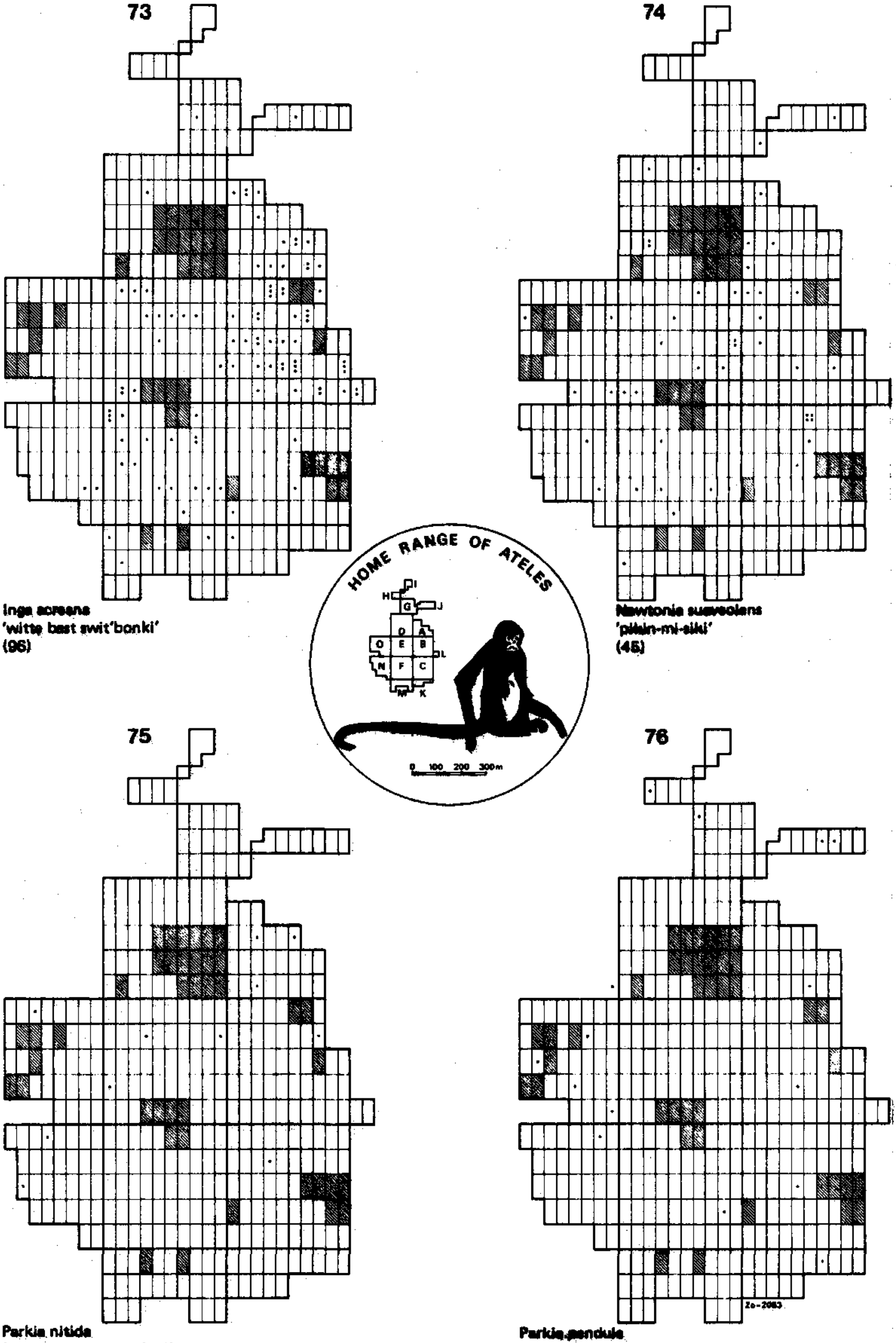
Inga edulis
'swit'bonki'
(19)

72



Inga leiocalycina
'swit'bonki'
(6)

HOME RANGE SHOWING DISTRIBUTION AND DENSITY OF FOOD PLANTS



73 Inga acreana
'witte bast swit'bonki'
(96)

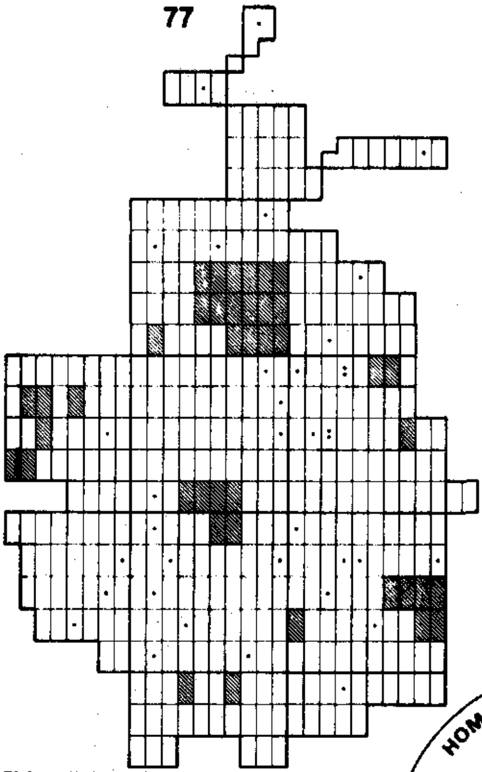
74 Newtonia suaveolens
'pikin-mi-siki'
(45)

75 Parkia nitida
'grootbloemige agrobigi'
(11)

76 Parkia pendula
'kwatakama'
(15)

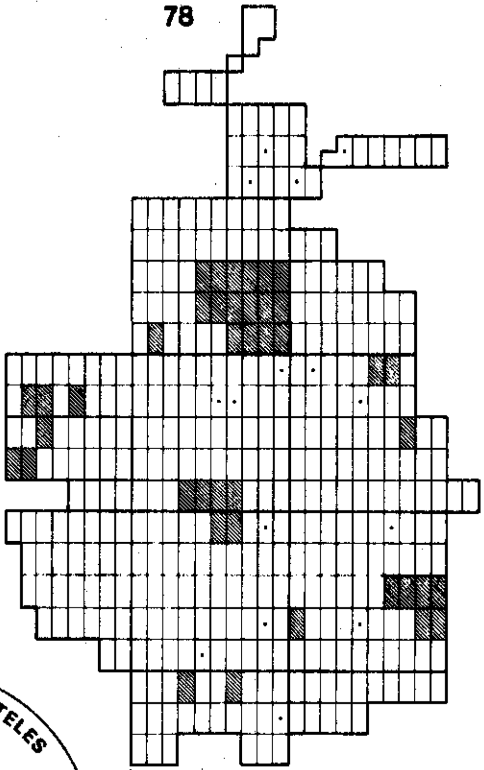
HOME RANGE SHOWING DISTRIBUTION AND DENSITY OF FOOD PLANTS

77

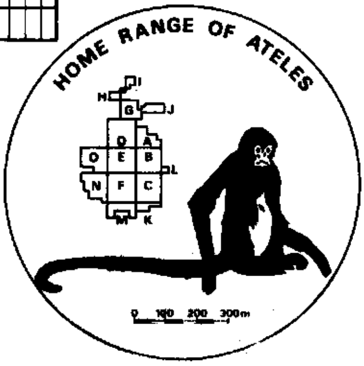


Pithecellobium jupunba
'fijnbladige sopo-oedoe'
(36)

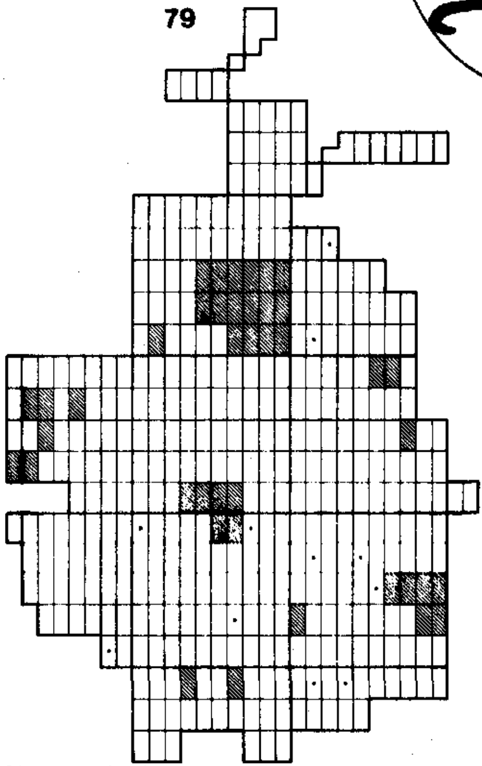
78



Stryphnodendron polystachyum
'hoogland lakairi'
(15)

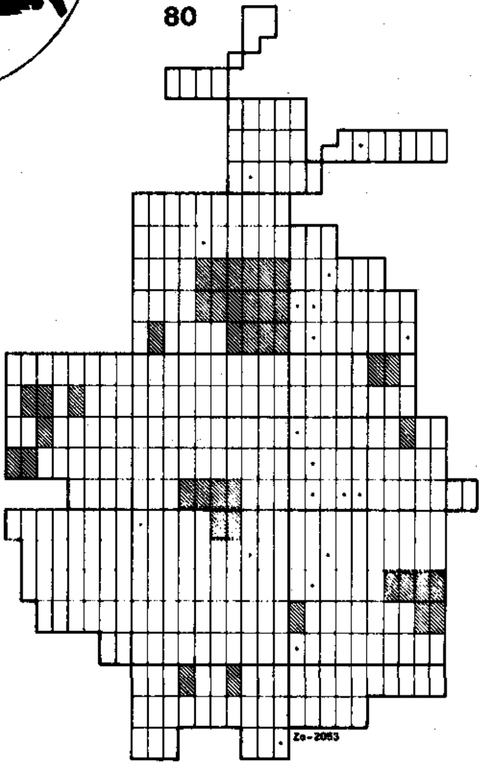


79



Dipteryx odorata
'tonka'
(11)

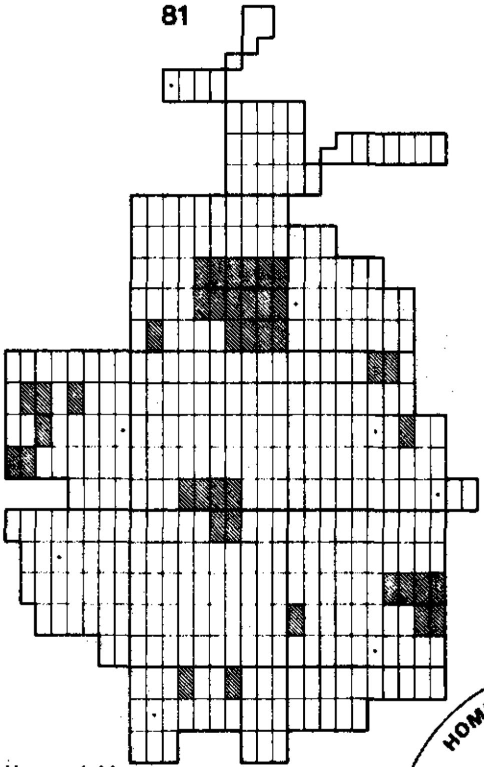
80



Hymenolobium flavum
'makakabes'
(19)

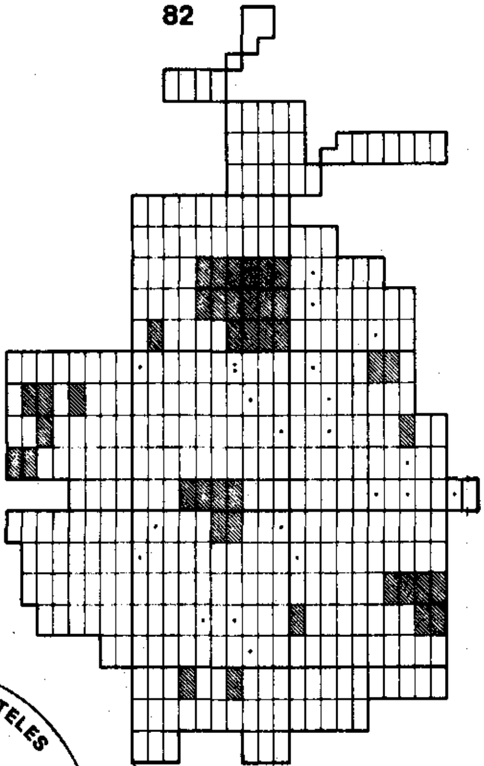
HOME RANGE SHOWING DISTRIBUTION AND DENSITY OF FOOD PLANTS

81

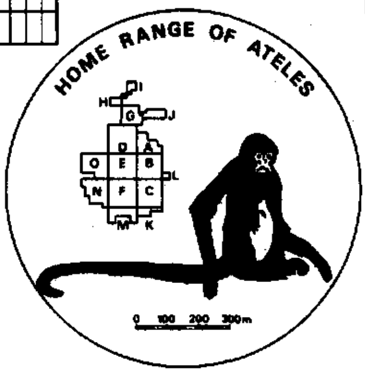


Hymenolobium petraeum
'wanakabes'
(8)

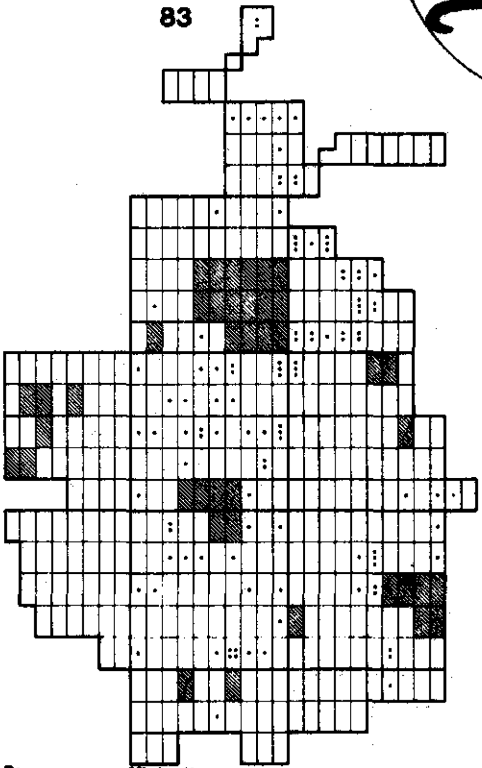
82



Platymiscium ulei
'koenatepi'
(22)

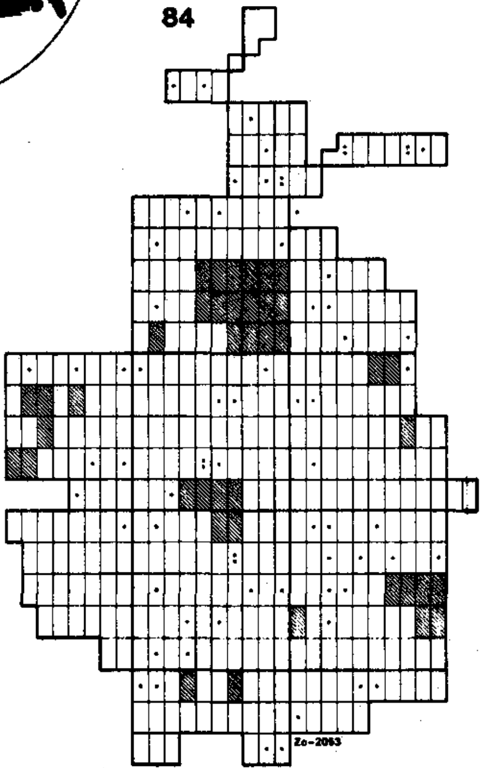


83



Pterocarpus officinalis
'watra-bebe'
(110)

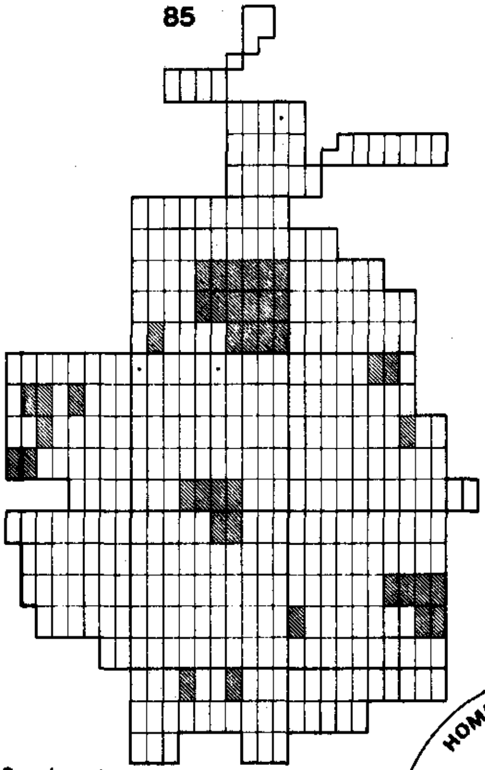
84



Vataireopsis speciosa
'djongokabes'
(70)

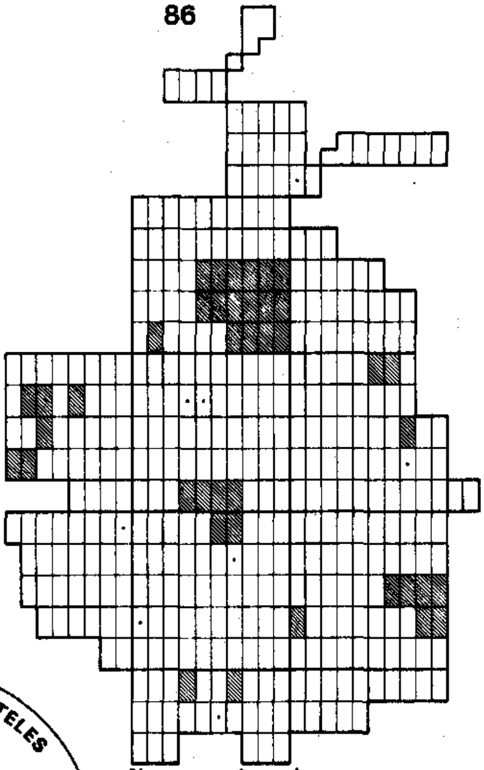
HOME RANGE SHOWING DISTRIBUTION AND DENSITY OF FOOD PLANTS

85

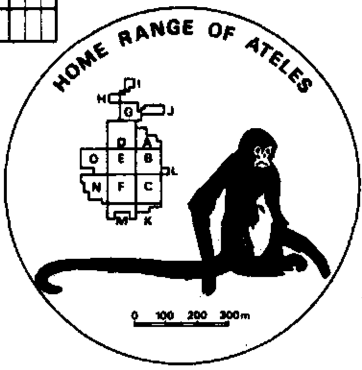


Strychnos tomentosa
'witte dobroedoewa'
(3)

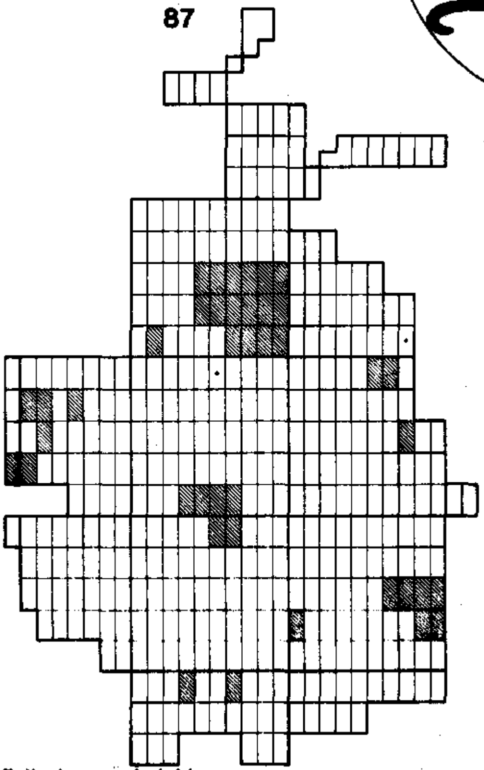
86



Norantea guianensis
'rafroe-tare'
(8)

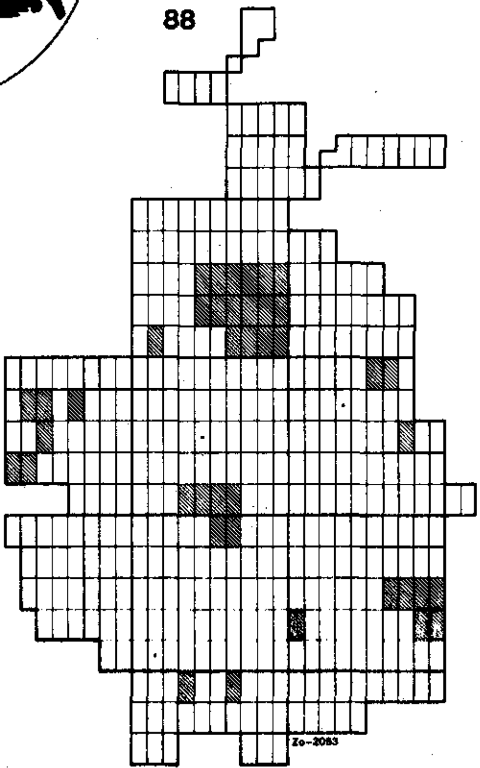


87



Bellucia grossularioides
'eetbare mispel'
(2)

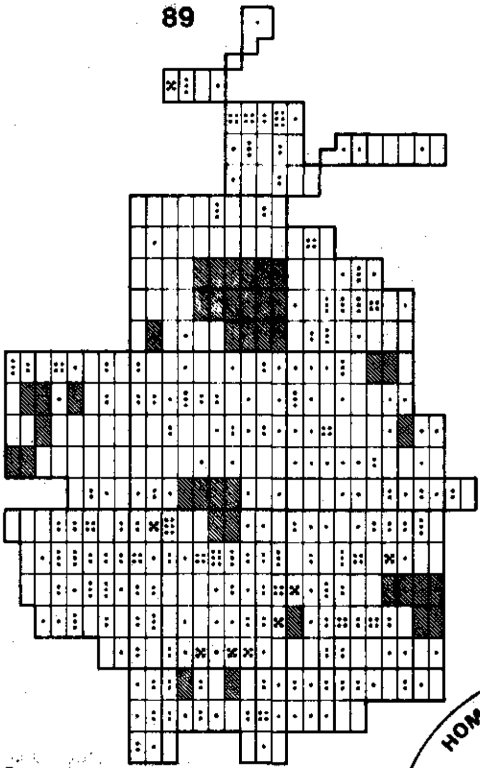
88



Mouriri sp.
'hoogbos spikri-oedoe'
(3)

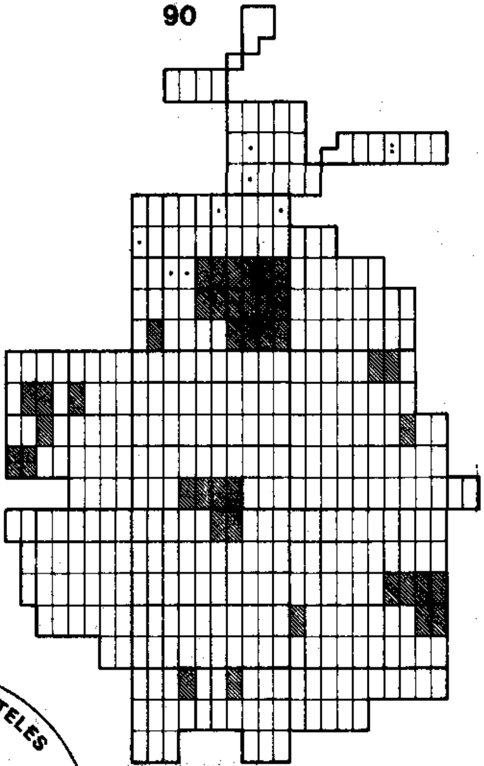
HOME RANGE SHOWING DISTRIBUTION AND DENSITY OF FOOD PLANTS

89

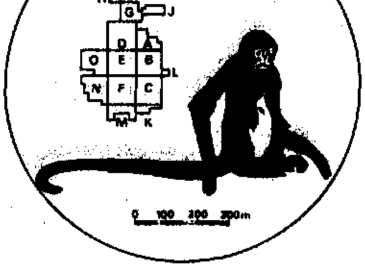


Carapa procera
'witte krapa'
(417)

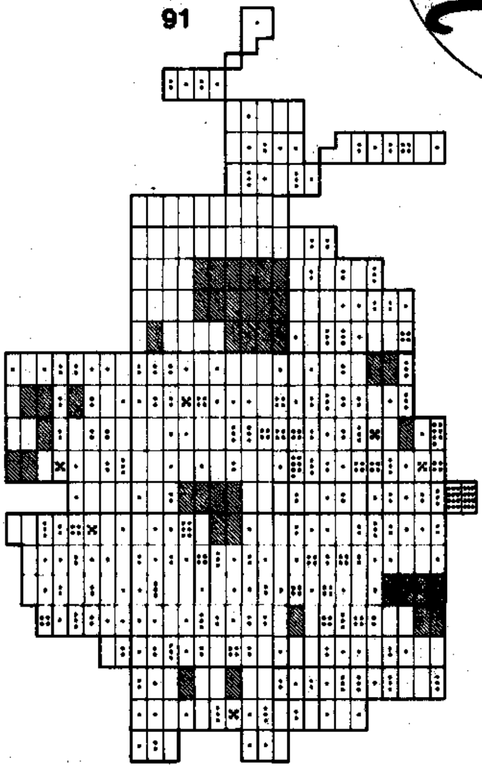
90



Cedrela odorata
'ceder'
(9)

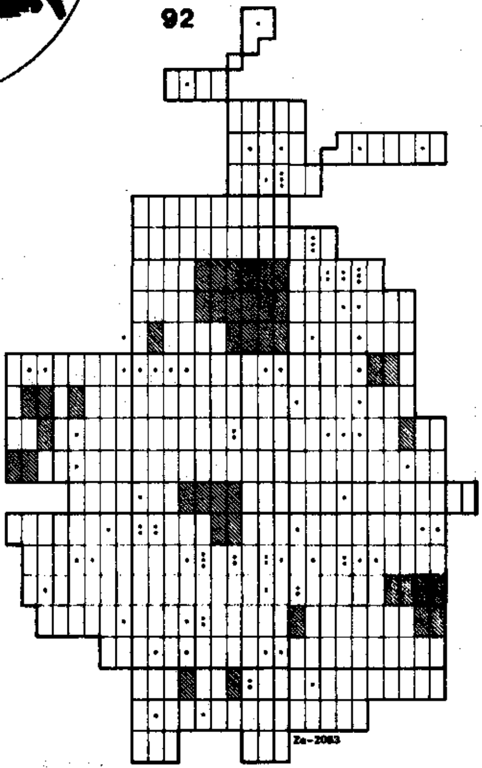


91



Guarea grandifolia
'doifisiri'
(449)

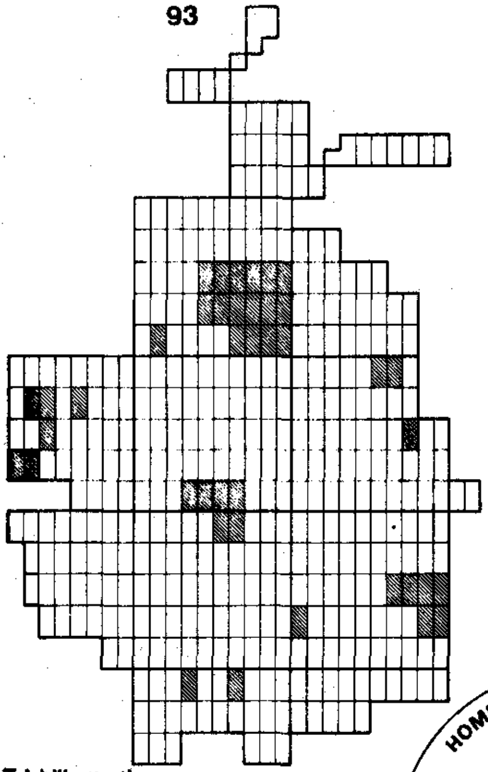
92



Guarea kunthiana
'zwarte doifisiri'
(88)

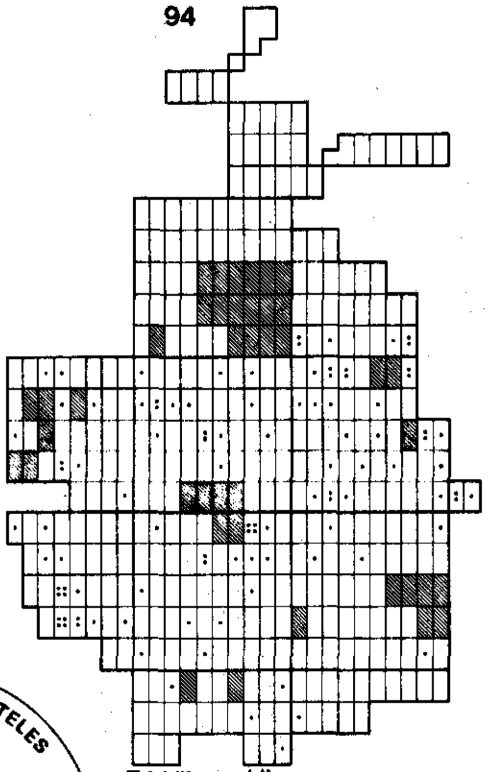
HOME RANGE SHOWING DISTRIBUTION AND DENSITY OF FOOD PLANTS

93

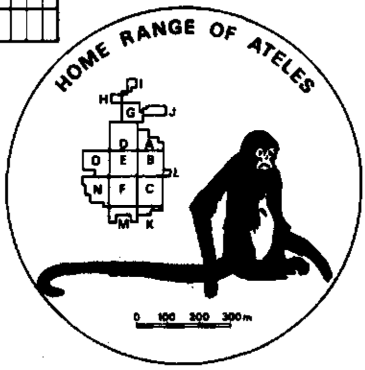


Trichilia martiana
(1)

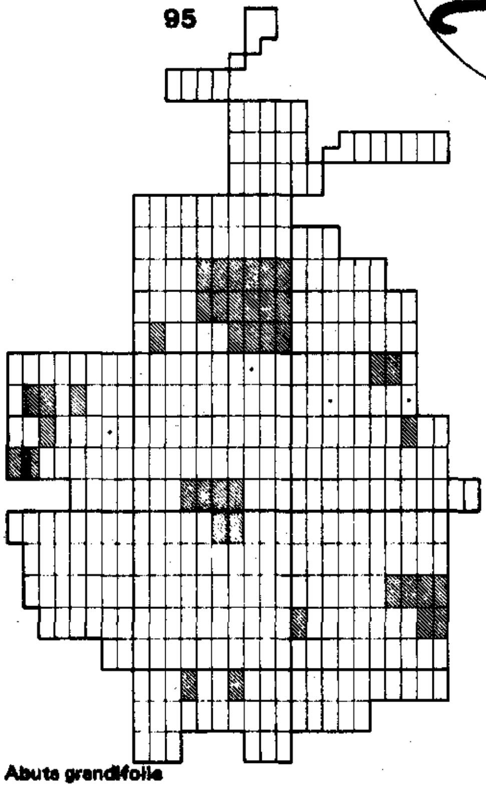
94



Trichilia quadrijuga
'sososali'
(102)

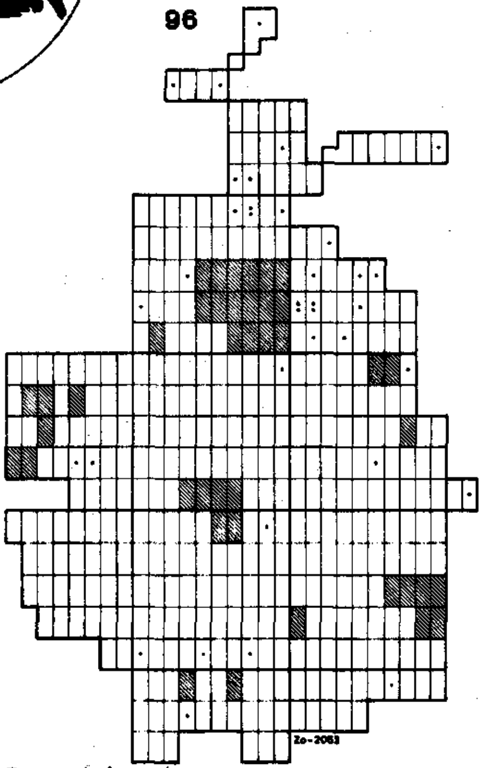


95



Abuta grandifolia
'bofroe-siri'
(4)

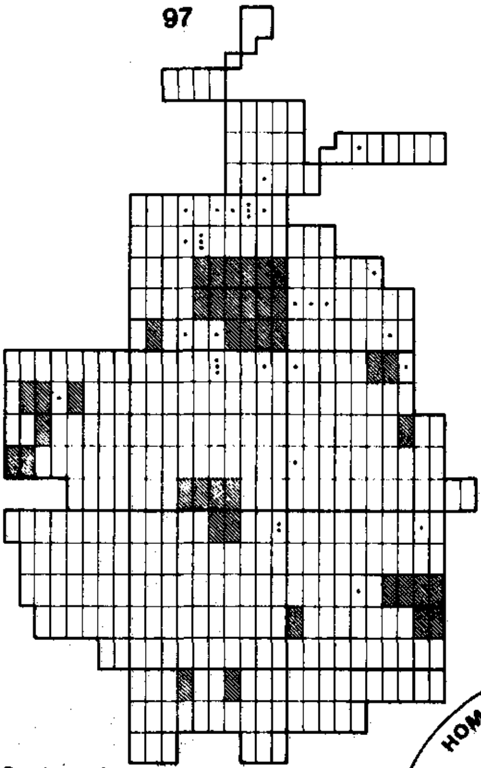
96



Bagassa guianensis
'kaw-oedoe'
(36)

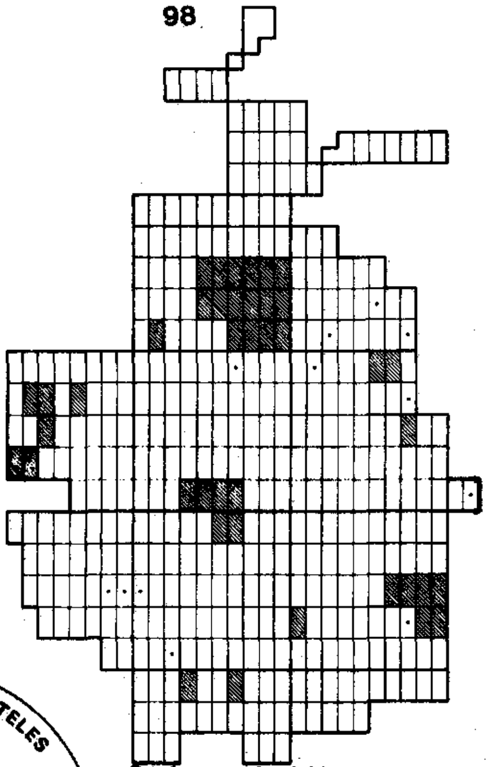
HOME RANGE SHOWING DISTRIBUTION AND DENSITY OF FOOD PLANTS

97

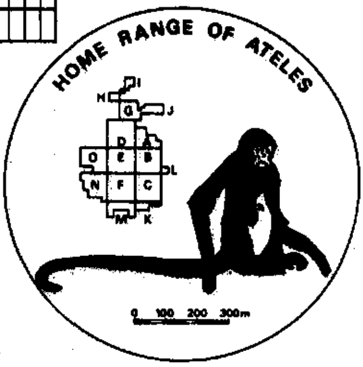


Brosimum lactescens
'kleinbladige dedikali'
(32)

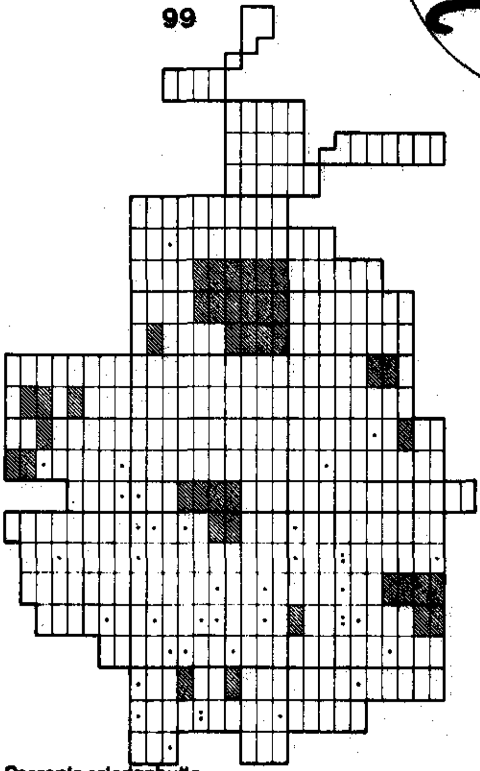
98



Brosimum parinarioides
'dedikali'
(12)

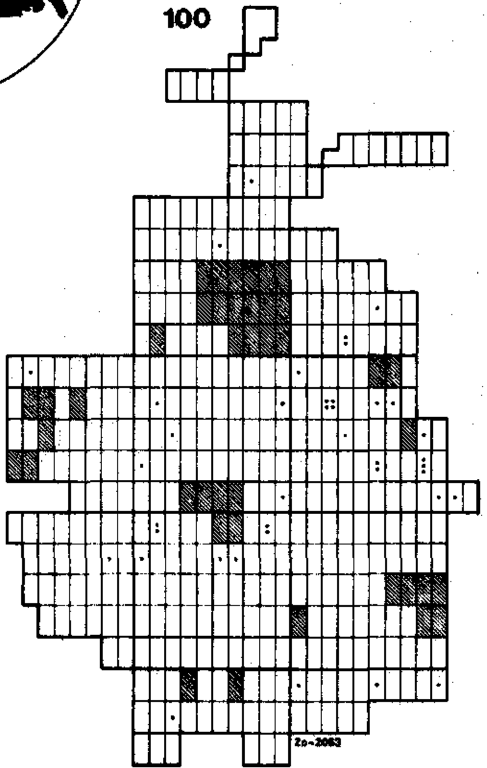


99



Cecropia sciadophylla
'man-bospapaja'
(40)

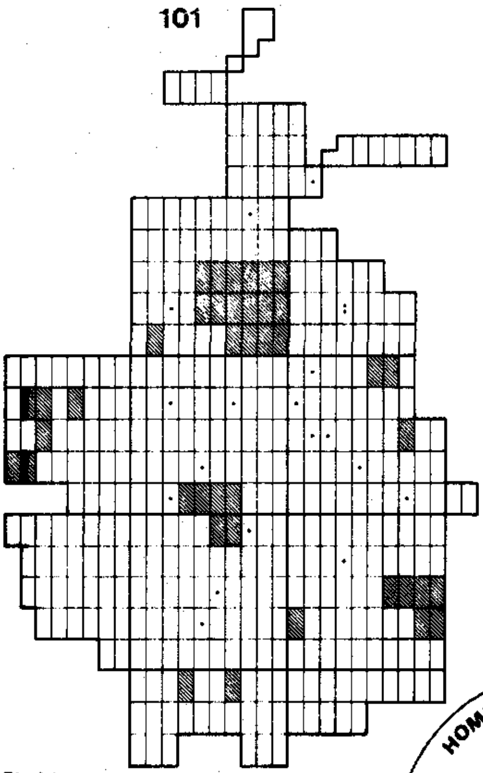
100



Cecropia surinamensis
'bospapaja'
(39)

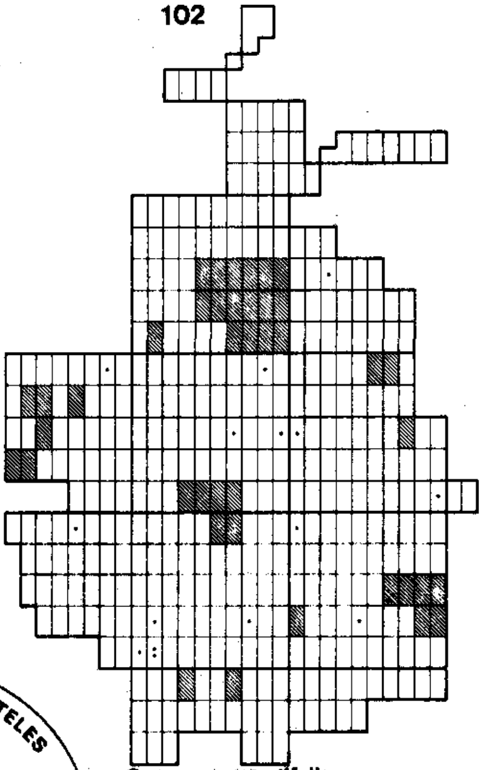
HOME RANGE SHOWING DISTRIBUTION AND DENSITY OF FOOD PLANTS

101

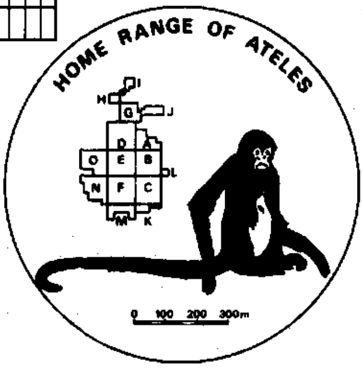


Clarisia racemosa
'rode bast doekali'
(19)

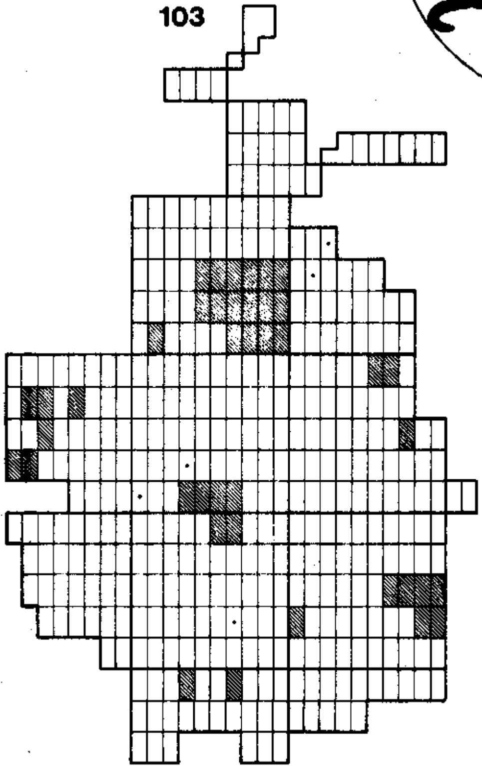
102



Coussapoa angustifolia
'bruinnerf-coussapoa'
(15)

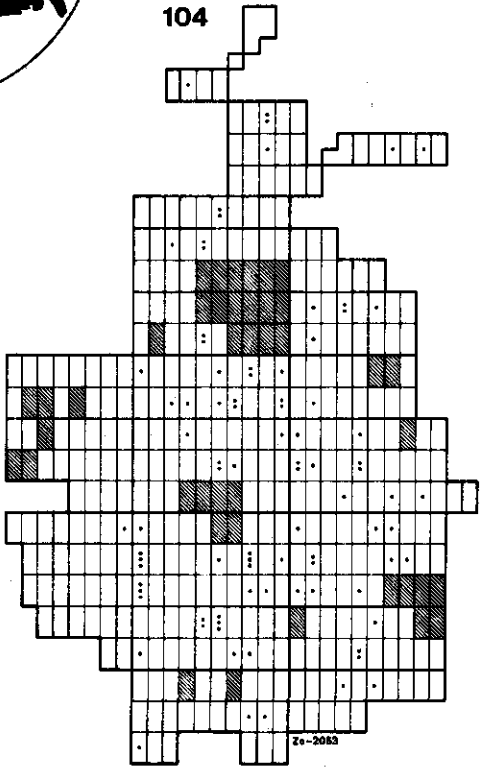


103



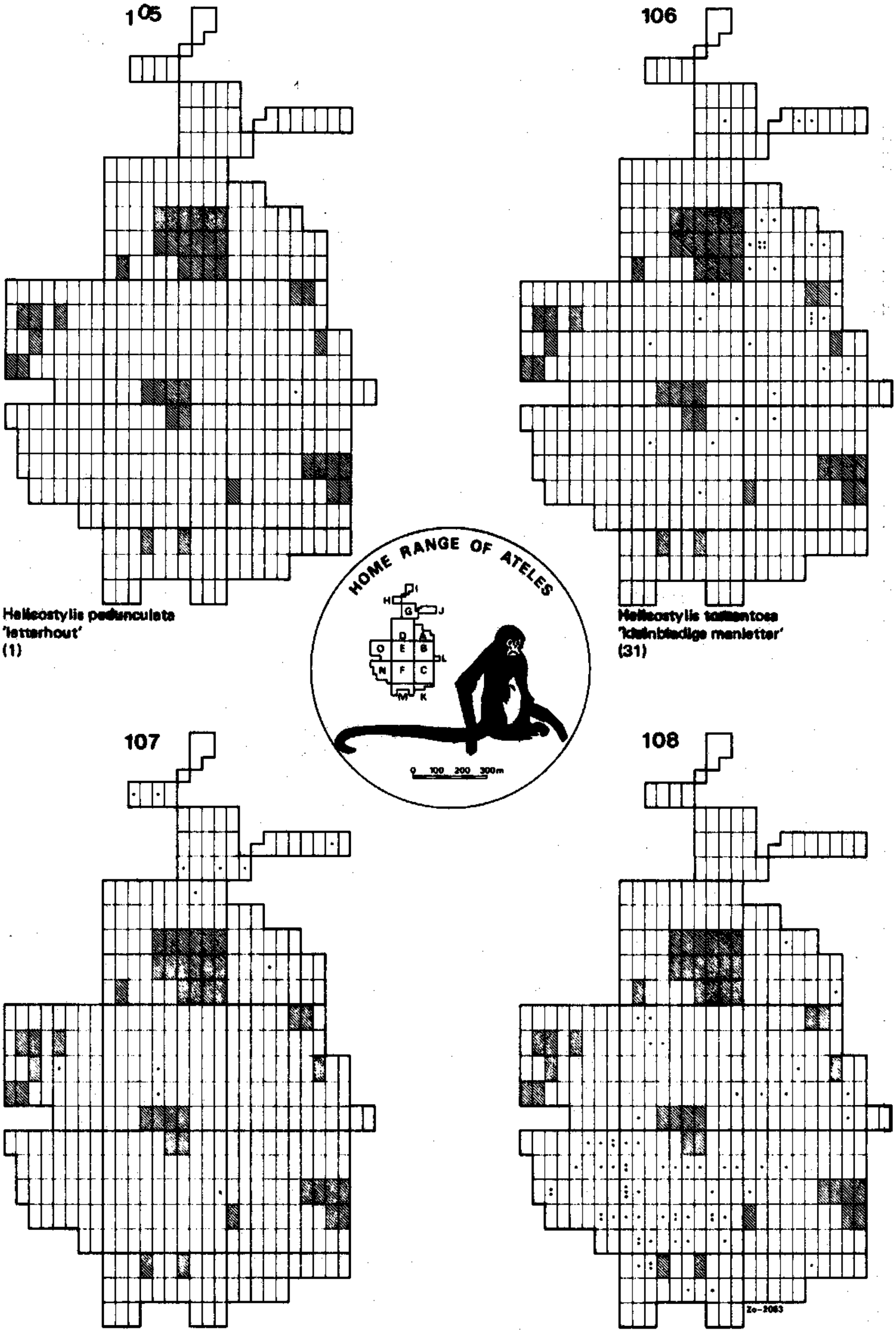
Coussapoa asperifolia
'ruwbladige coussapoa'
(5)

104



Coussapoa latifolia
'gladbladige coussapoa'
(86)

HOME RANGE SHOWING DISTRIBUTION AND DENSITY OF FOOD PLANTS



105

Helicostylis pedunculata
'letterhout'
(1)

106

Helicostylis tomentosa
'kleinbladige manletter'
(31)

107

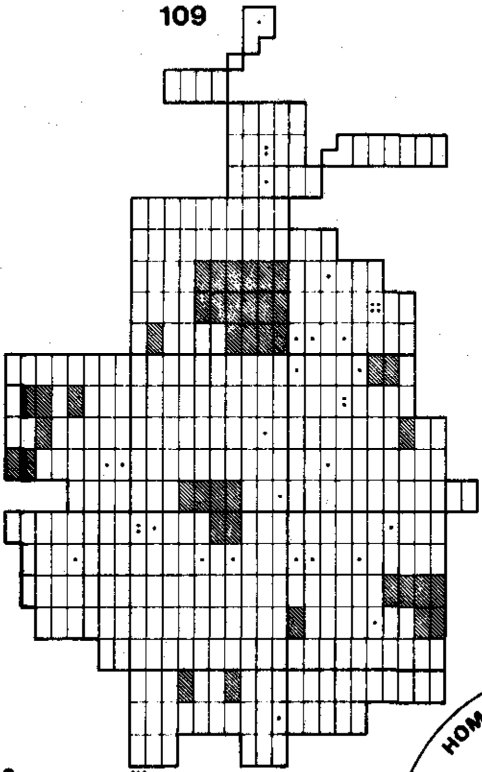
Maquira guianensis
'gewone manletter'
(12)

108

Pourouma minor
'granboesi-papaja'
(64)

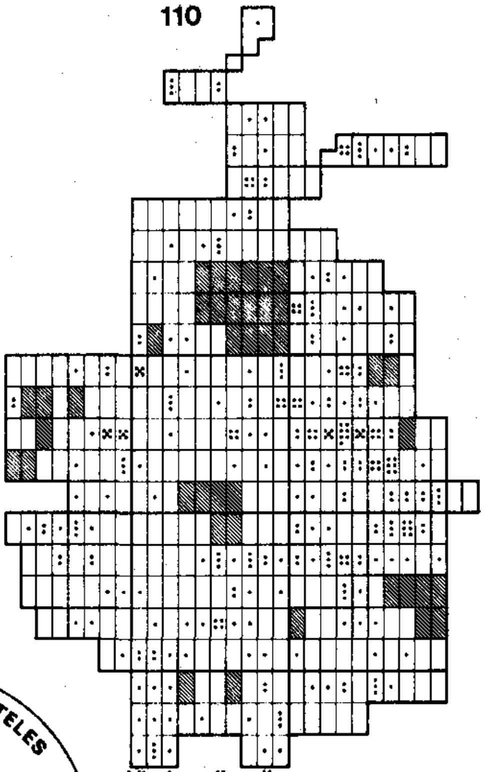
HOME RANGE SHOWING DISTRIBUTION AND DENSITY OF FOOD PLANTS

109

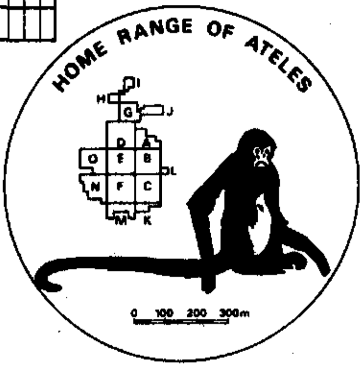


Pourouma mollis
'granboesi-papaja'
(33)

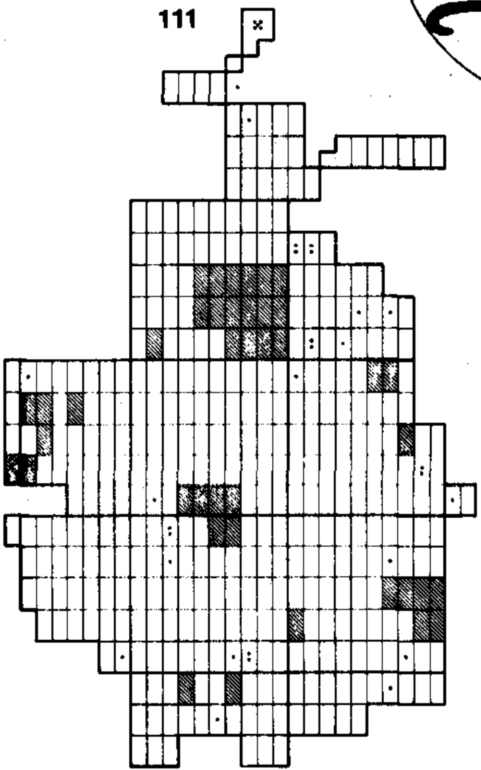
110



Virola melinonii
'hoogland baboen'
(313)

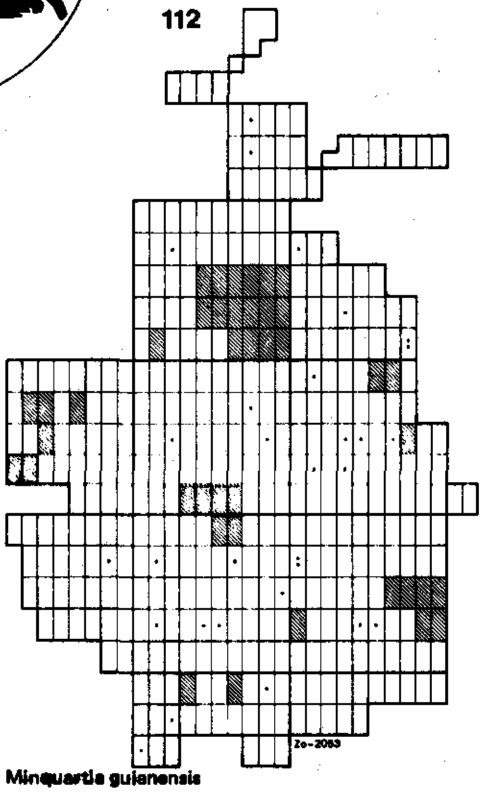


111



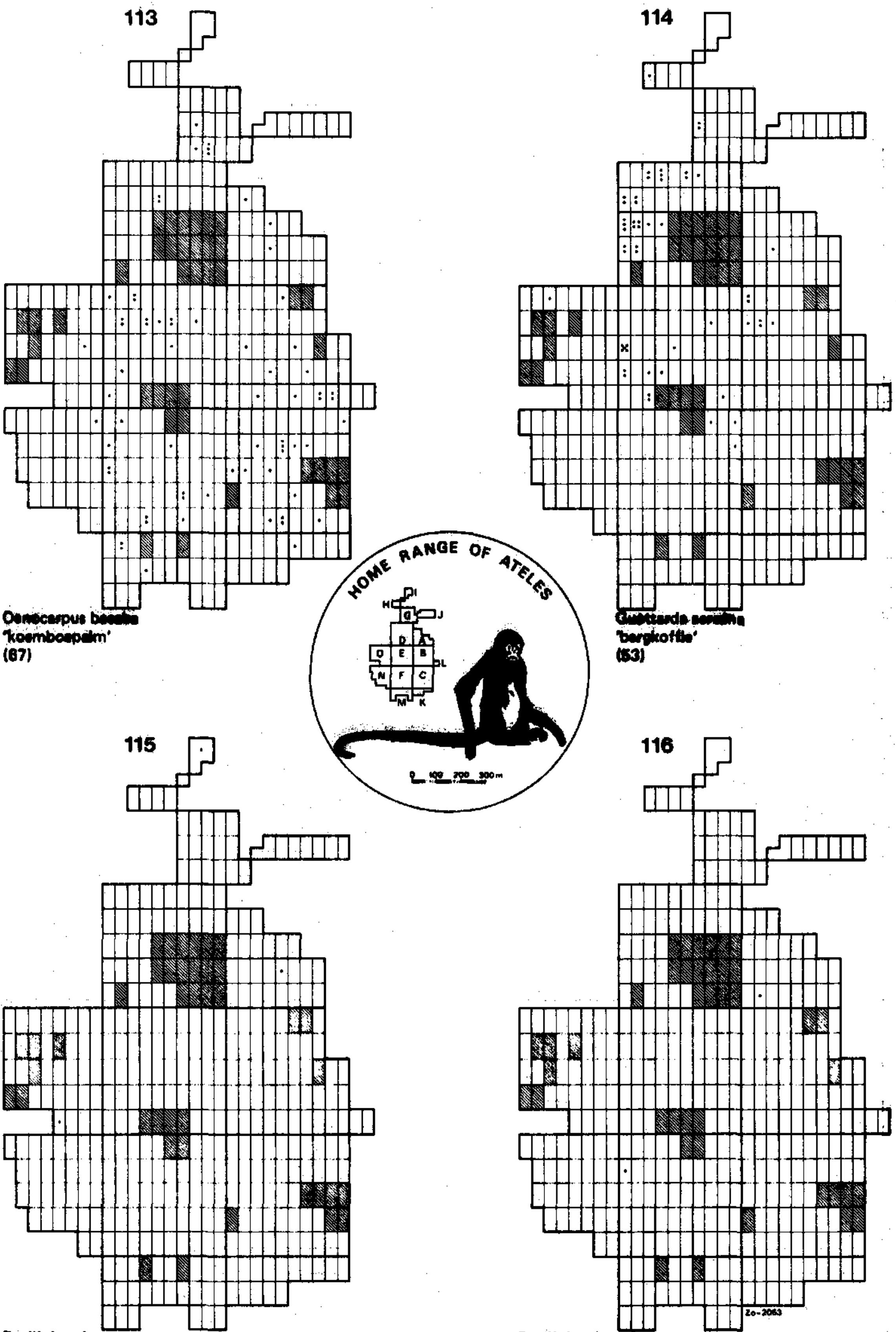
Virola surinamensis
'laagland baboen'
(32)

112



Minquartia guianensis
'alata-oedoe'
(30)

HOME RANGE SHOWING DISTRIBUTION AND DENSITY OF FOOD PLANTS



113: Oenocarpus bacaba
'koemboepalm'
(67)

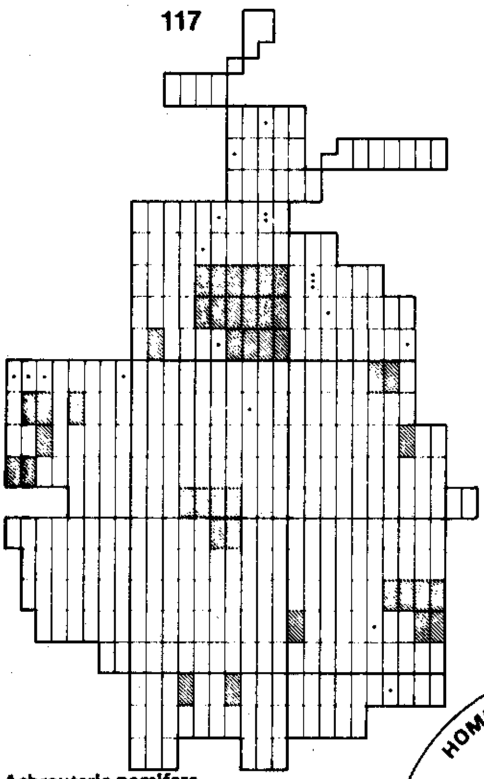
114: Guettarda acreana
'bergkoffie'
(53)

115: Paullinia spicata
'fefi-finga'
(3)

116: Paullinia tricornis
(2)

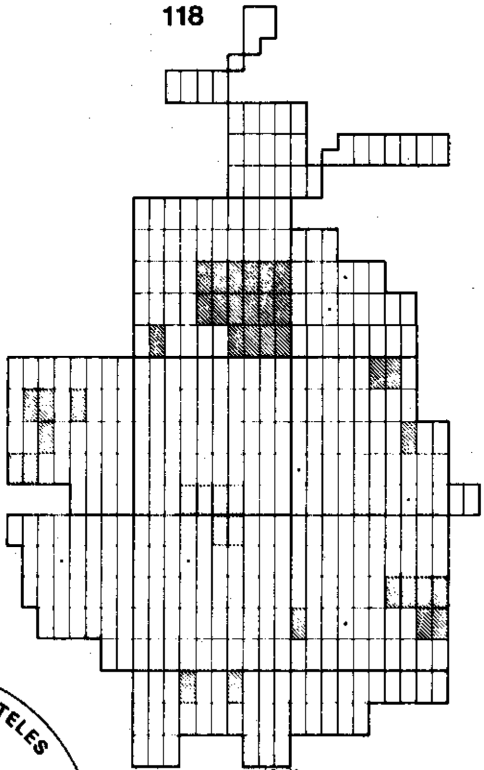
HOME RANGE SHOWING DISTRIBUTION AND DENSITY OF FOOD PLANTS

117

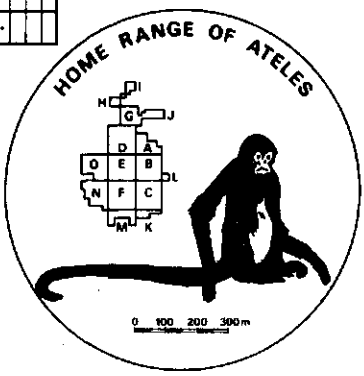


Achrouteria pomifera
'hoogland kimboto'
(19)

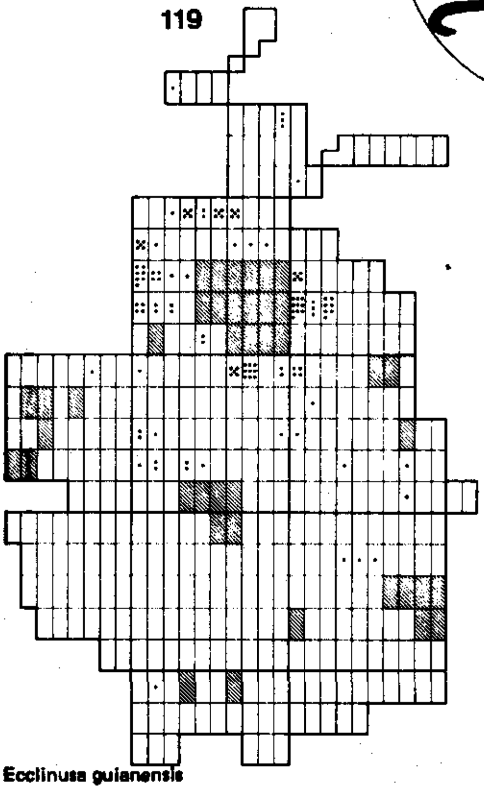
118



Ecclinusa cuneifolia
'kwatabobi'
(7)

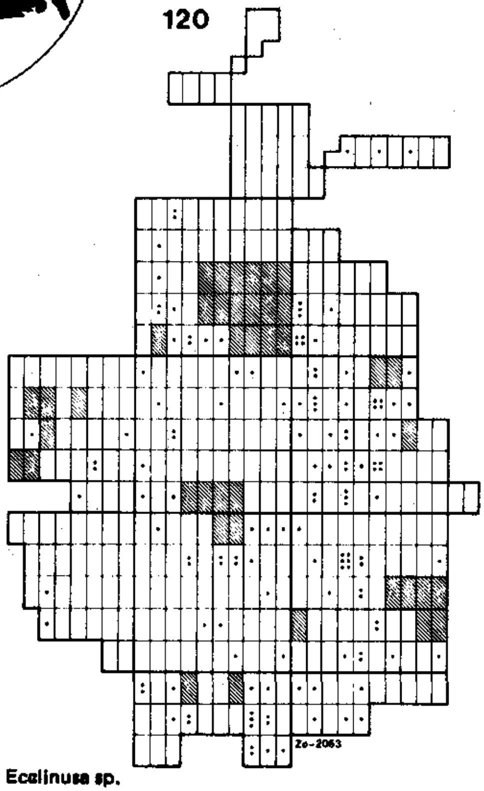


119



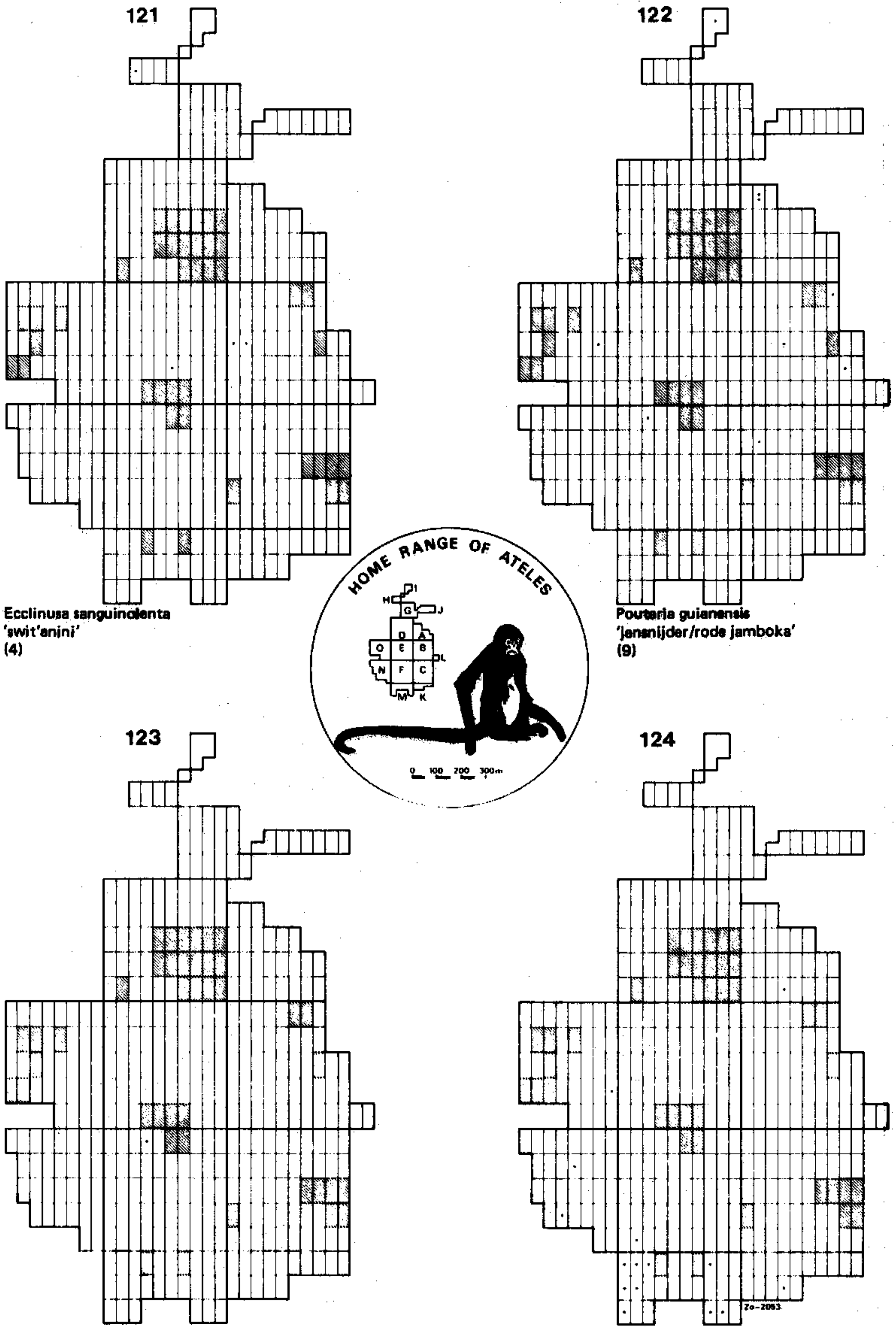
Ecclinusa guianensis
'batambali'
(121)

120



Ecclinusa sp.
'hoogland kimboto'
(138)

HOME RANGE SHOWING DISTRIBUTION AND DENSITY OF FOOD PLANTS



121
Ecclinusa sanguinolenta
'swit'anini'
(4)

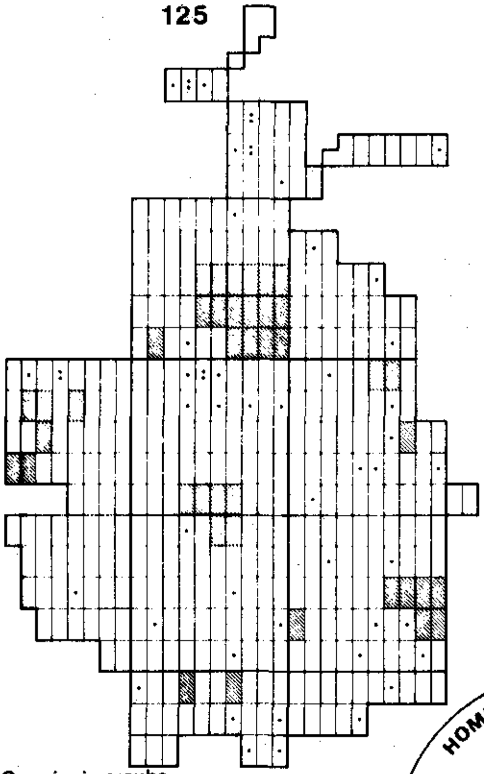
122
Pouteria guianensis
'jensnijder/rode jamboka'
(9)

123
Pouteria sagotiana
'apra-oedoe'
(1)

124
Pouteria sp. nr. 400
(15)

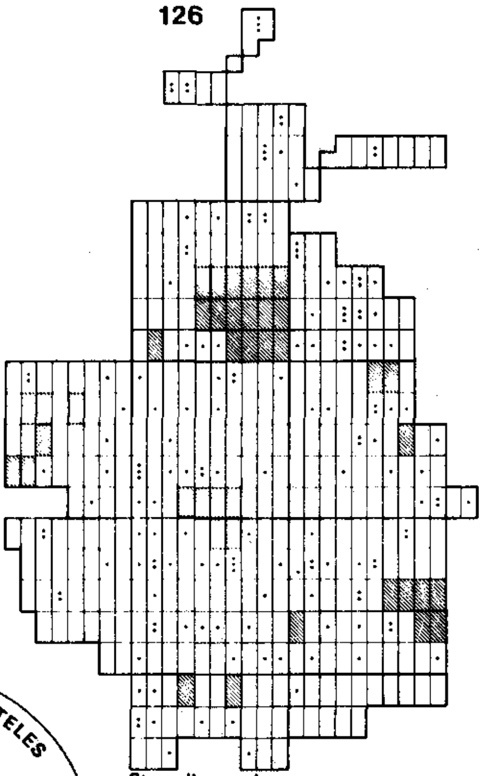
HOME RANGE SHOWING DISTRIBUTION AND DENSITY OF FOOD PLANTS

125

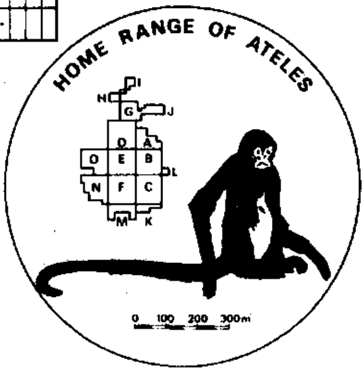


Quassia simarouba
'soemaroeba'
(53)

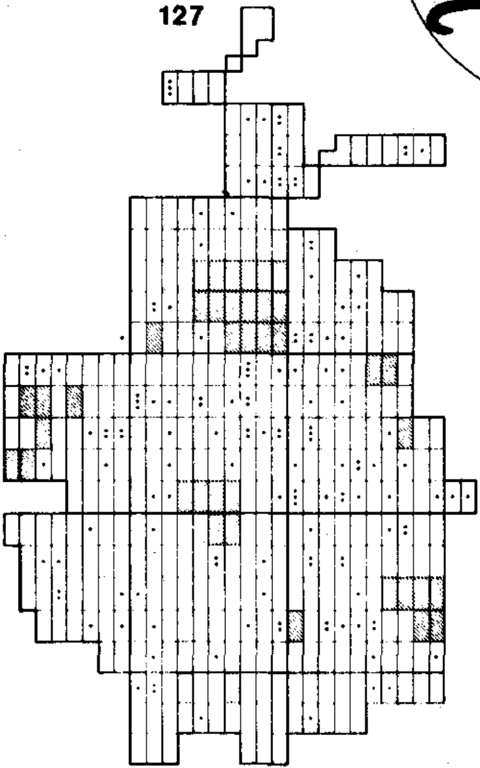
126



Sterculia excelsa
'okro-oedoe'
(155)

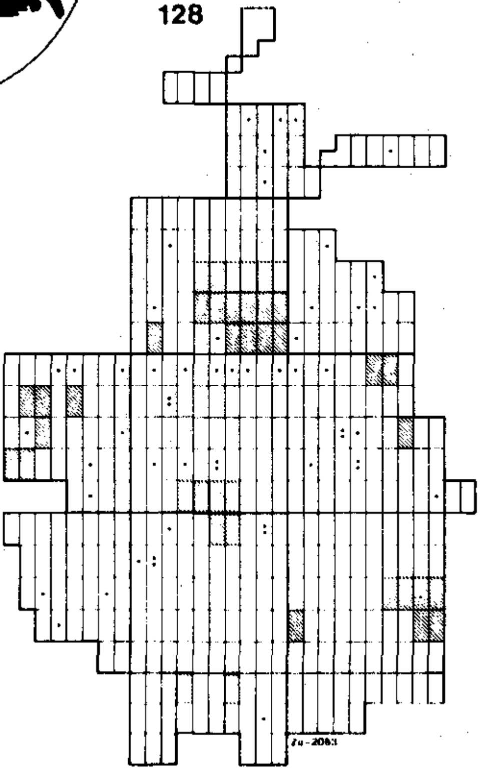


127



Apeiba echinata
'kankan-oedoe'
(145)

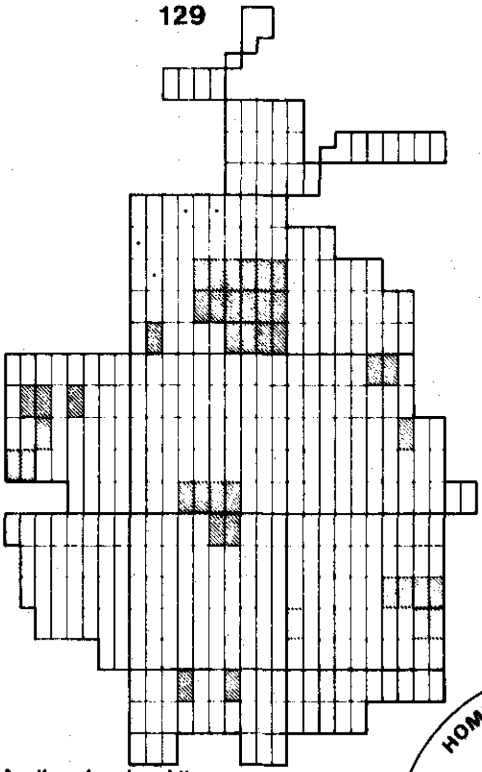
128



Apeiba glabra
'kankan-oedoe'
(54)

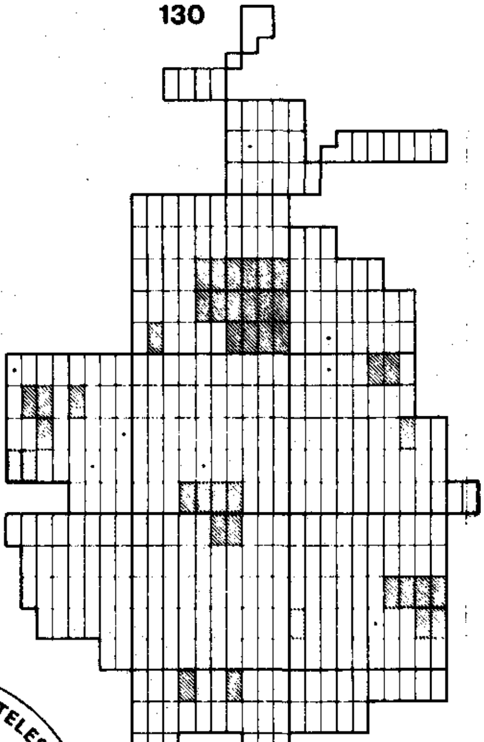
HOME RANGE SHOWING DISTRIBUTION AND DENSITY OF FOOD PLANTS

129

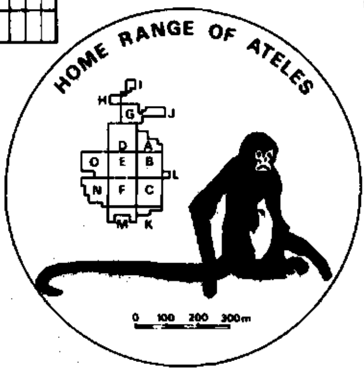


Apeiba schomburgkii
'kankan-oedoe'
(4)

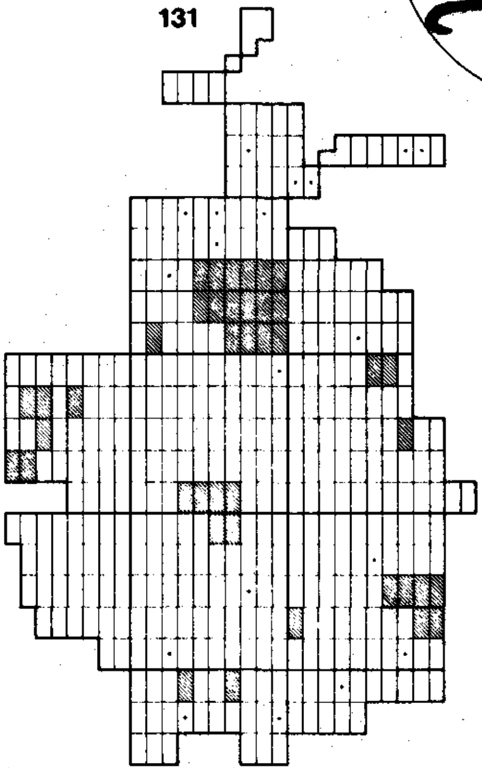
130



Apeiba tibourbou
'fofofoko-oedoe'
(8)

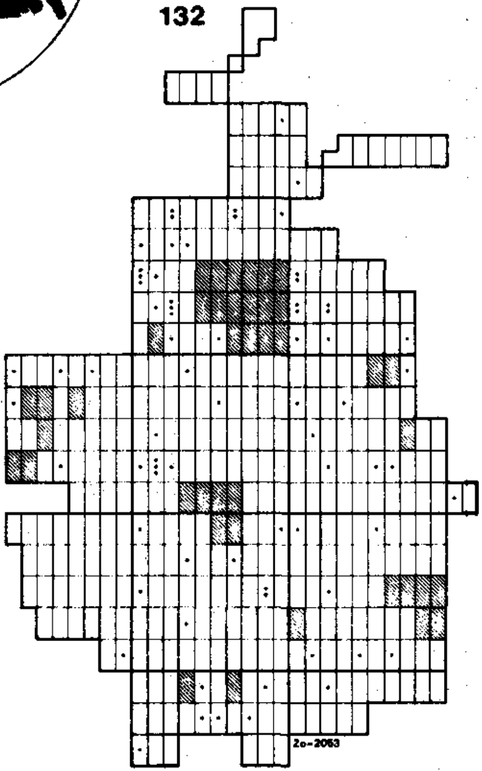


131



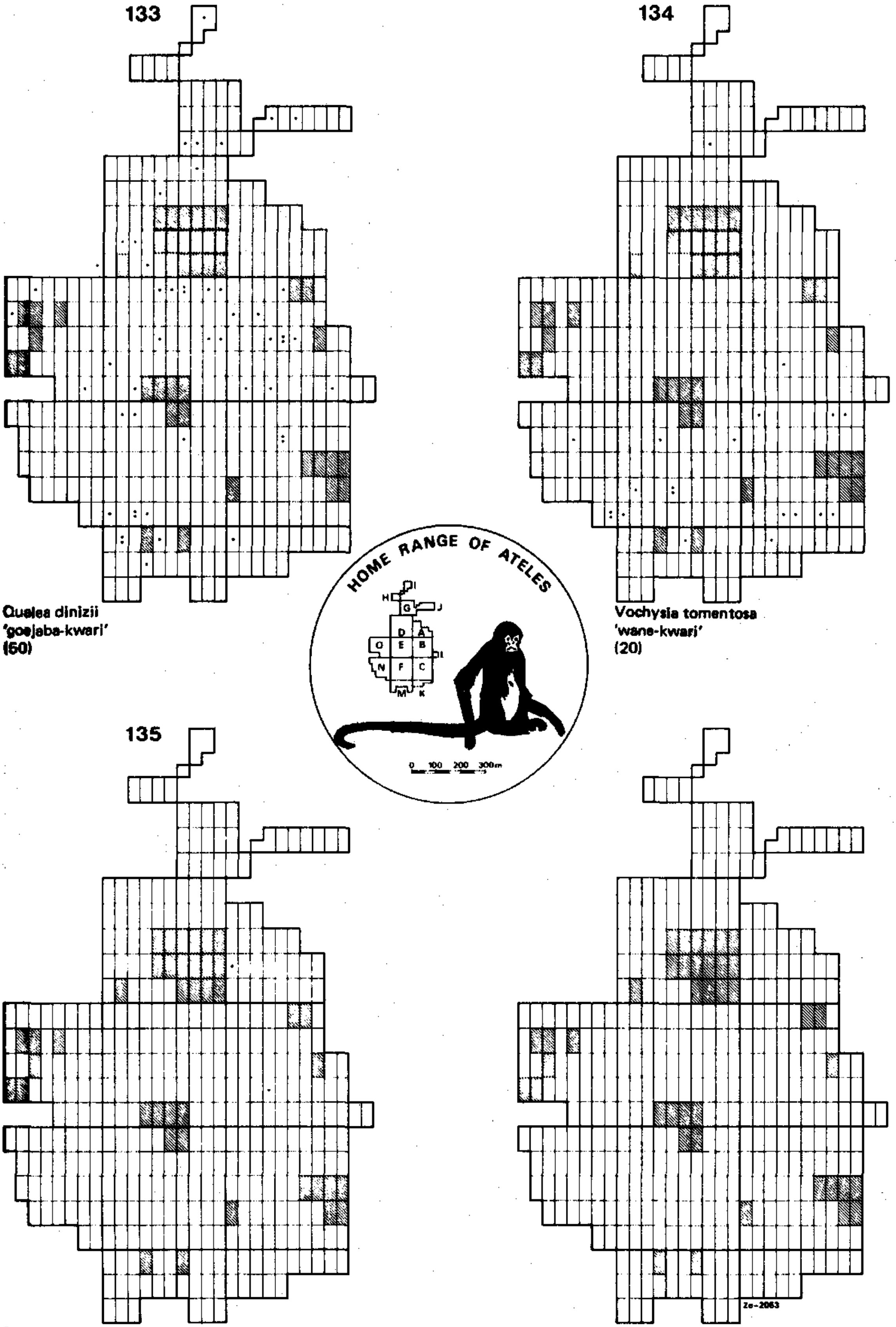
Ampelocera edentula
'kwas'kwas'oedoe'
(19)

132



Vitex stahelii
'kalebashout'
(72)

HOME RANGE SHOWING DISTRIBUTION AND DENSITY OF FOOD PLANTS



133

Qualea dinizii
'goejaba-kwari'
(60)

134

Vochysia tomentosa
'wane-kwari'
(20)

135

Styrax cf. fanshawei
(2)