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ANIMAL SEED-DISPERSERS AS KEY ELEMENTS FOR CONSERVATION OF TROPICAL FORESTS:

A case study in the Nyungwe Forest Reserve, Rwanda

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EXECUTIVE SUMMARY

The goal of this project is to contribute to the conservation of tropical forests, particularly those forest which will not be in reserves. The challenge is to develop management approaches to such diverse forests which will allow for exploitation of forest resources while simultaneously maintaining the natural diversity of biological resources.

Seed dispersal is a critical step in the natural regeneration of tropical forests. The pattern of dispersal of tree seeds is likely to have an important influence on the future tree species composition of the forests and hence on the natural diversity associated with those tree species. Animal seed-dispersers are considered to be important agents for the dispersal of the seeds of the majority of tropical tree species. This study is aimed at defining the role of several species of animal dispersers in the dispersal of the ecologically and economically important tree species of the Nyungwe Forest of Rwanda. The Nyungwe Forest is an appropriate target for such a study since it is one of the richest remaining islands of montane forest in central Africa. However, the population and political pressure will require that the forest provide benefits in the form of forest products. A management plan is needed for Nyungwe which can allow exploitation while maintaining the natural biodiversity.

This study was able identify the important tree seed dispersers, monkey and bird species, using a multi-faceted approach. With two Rwandan senior scientists, one Rwandan student, three American students, and one chinese student, we were able to amass an impressive array of data encompassing over 50 species of trees and some 20 species of animal seed dispersers. These data include some basic background ecology data of the forest such as analysis of the forest vegetation and a monthly, long-term record of seasonal pattern of fruiting of the forest trees. From the tree perspective we conducted systematic watches of fruiting trees to determine the set of potential seed dispersers visiting the trees. We used direct follows of selected animal fruit-eaters to determine the set of fruit resources used by those animals and the movement patterns of these animals through patches of closed canopy forest and forest clearings. These observations allowed us to assess the relative importance of different animals in moving seeds through the forest and facilitating forest regeneration. Small, inconspicuous understory birds, bulbuls, were shown to be effective dispersal agents for a wide variety of forest trees and shrubs. One species of monkey, already rare in most of central Africa, appeared to be an important agent for moving seeds from forest trees into clearings.

The findings of the three years of the project have provided ideas for future work which will move closer to developing innovative management techniques. For example, we believe we can show that certain trees in open clearings attract fruit-eating animals out of the forest to eat their fruits. These animals in turn are likely to deposit seeds in the openings which they ate inside the forest. Some relatively simple manipulations of vegetation in degraded portions of the forest may take advantage of animal dispersers to enhance the rapidity and diversity of natural regeneration.

The study involved a close collaboration with Rwandan botanists and ecologists. This included training of a Rwandan university student, working with Rwandan forestry officials to incorporate the perspectives of this study in future forest management plans now being developed, and working with a Rwandan research institute to reinforce their efforts to expand research on conservation of biodiversity and its importance maintaining forest resources and sustainable development options.

PREAMBLE

This study has included an unusually wide and diverse set of research approaches and has been directed not only at the research agenda but also at institution building and the developing of future research options to more closely approach the principal goal of contributing toward the sustainable management and conservation of tropical forests. The data set collected is very large, very diverse, and will take substantially more time to be analyzed and interpreted. Nevertheless, this process is moving ahead simultaneously with the implementation of new research efforts at the same site which have been derived from the present project. This report cannot be comprehensive at this time, but it will attempt to give an accurate representation of the extent of this research effort and the nature and application of preliminary findings.

RESEARCH OBJECTIVES

OVERALL AIM:

The principal goal of this project is to conserve the great diversity of biological resources of tropical forests using as a model the Nyungwe Forest of Rwanda in central Africa. The special focus of this study is the conservation of animal seed dispersers of the forest trees as important functional elements in the natural regeneration dynamics of the forest. Although the mutual interaction of forest trees and their dispersers is widely recognized, rarely, if ever, have forest management plans been adjusted to conserve this interaction as part of the conservation/management of natural tropical forests. We believe this lack of application is largely due to the lack of information on the role of animal forest seed-dispersers and the absence of site specific information needed to incorporate these animals in an appropriate management plan. Our specific objectives of this project were aimed at providing the basic information useful for the development of a forest management plan.

SPECIFIC OBJECTIVES:

Step 1: We intended to answer the following questions as completely as possible within the constraints of a small project and only three years of study.

1) Which of the ecologically and economically important tree species depend on animals to disperse their seeds?

2) Which animal species are needed as dispersers of these trees?

3) Which fruiting trees (and other forest resources) need to be maintained as critical food sources for the animal dispersers?

Complete answers to these questions would need many years of intensive study by many researchers. Our intent was to provide enough information to convince concerned officials and resource/forest managers of the value of animal seed-dispersers, to document the nature and extent of their contribution to forest dynamics, and to provide a clearer picture of the needs of the animals and the ecological elements and/or factors necessary to consider in forest management.

Step 2: We view the process of collecting information about the three specific questions above as a useful mechanism for gaining new information and developing new insights into the ecology of the animal disperser/tree regeneration interaction which would be useful for designing future studies to develop effective and innovative forest management approaches incorporating animal dispersers (see section below on Future Work).

THE RESEARCH TEAM

This study has involved a complex, extensive contribution from many different researchers and students. The principal contributors are listed below with their institutions. The researchers with primary responsibility for a given research method/approach is indicated below under Methods and Results.

P.I. Timothy C. Moermond, Ph.D., Professor of Zoology and Environmental Studies, University of Wisconsin-Madison, Madison, Wisconsin. (Scientific advisor to Sun, Kaplin, Kristensen, and Graham)

Co-P.I. Joseph Mvukiyumwami, Ph.D., Senior researcher, Institut de Recherche Scientifique et Technologique, Butare, Rwanda.

Co-P.I. Kanyonyo ka Kajondo, Ph.D., Professor of Biology, Universite Nationale du Rwanda, Butare, Rwanda. (Scientific advisor to Munyaligoga)

Chin Sun, Ph.D. candidate, Department of Zoology, University of Wisconsin-Madison, Madison, Wisconsin.

Beth Kaplin, M.S. and Ph.D. candidate, Department of Zoology, University of Wisconsin-Madison, Madison, Wisconsin.

Kurt Kristensen, M.S. candidate, Land Resources Program, Institute for Environmental Studies, University of Wisconsin-Madison, Madison, Wisconsin.

Viateur Munyaligoga, License candidate, Departement de Biologie, Universite Nationale du Rwanda, Butare, Rwanda.

Catherine Graham, B.S. student, Eckerd College, St.Petersburg, Florida.

Additional consultation and advice has been provided by two other intended co-investigators:

Amy Vedder, Ph.D., Research Associate, Wildlife Conservation Society, New York Zoological Society, Bronx Zoo, Bronx, New York.

Samuel Kanyamibwa, Ph.D., Researcher, Project of Conservation of the Forest of Nyungwe and Professor of Biology, Universite Nationale du Rwanda, Butare, Rwanda.

METHODS AND RESULTS

Tropical forests are extraordinarily complex and, as yet, extremely poorly known. We could not study all aspects of the animal seed-dispersers/tree regeneration interaction, nor can all aspects be studied with equal precision. We chose to take a selective, multi-faceted approach to answer our specific questions. We selected a series of different research approaches with the intent that the diverse information provided by each approach would complement and augment the results of the other approaches. The approaches described here represent the final series which has been modified and enlarged during the course of the three year study.

I. METHODS/DATA COLLECTED:

1) Forest Plant Phenological Studies: (Sun, Kaplin, Kristensen, Mvukiyumwami)

Method: The condition of leaves (mature, new, senescent, dropped) and reproductive stage (buds, flowers, unripe and ripe fruit) of all trees are recorded monthly in the phenology survey. Each category is recorded as a percentage of the total canopy volume or as a percentage of the maximum quantity that the tree can potentially produce and is placed into one of five scales: 0=none, 1=1-25%, 2=26-50%, 3=51-75%, 4=76-100%. Frequent comparisons of scores between observers ensures a high level of consistency. The reproductive capacity of a tree is assumed to be related to the size (volume) of its crown which has been shown to be correlated with the its' DBH (Peters et al. 1988). The fruit production of a species at any month can be expressed by summing the fruit scores of all conspecific individuals weighted by their DBHs.

For each species of tree at least 10 reproductively mature individuals are chosen, measured (DBH, height), and permanently marked. The steep topography of Nyungwe forest allows one to clearly see the crown of many trees from trails cut along contour lines. On the third week of each month, all marked trees along designated routes are monitored and scored according to the criteria listed above.

Data collected: We now have 2 and 1/2 years of phenology data on 600 trees of 50 species. (including phenology of ca 30 individuals each for Ekebergia and Syzygium in the past 18 months to examine the within species variation in phenology of two important fruit-producing species).

2) Vegetation Analysis: (Sun, Kaplin, Mvukiyumwami)

Method: A vegetation map was drawn of the study site delineating all vegetation types which could be reliable recognized and separated from other types by objective criteria. Within each zone, .1 ha vegetation plots (50m X 20m) were randomly placed and permanently marked. Overall placement was by a stratified random procedure to ensure proportion representation of each vegetation type. The validity of the recognized vegetation types will be tested by the results of the vegetation analysis. All trees (>50 DBH) in the plot were identified, measured, marked, and mapped. Within the plot, designated subplots were used to measure the shrub and herb layer. Five 5m X 5m plots were used to record all stems of saplings, shrubs, and lianas. Twenty 1m X 1m plots (arranged in groups of 5 consecutive plots) were used to record all stems of herbs, seedlings, and grasses.

Data collected: We have completed sampling eighty-two 0.1 hectare vegetation plots in our study site.

3) Focal Tree Observations: (Moermond, Sun, Kaplin, Kristensen, Munyaligoga, Kanyonyo, Graham)

Method: Selected trees with fruit crops were observed systematically for prescribed periods of time of 1, 3, or 8 hours. Within the tree watches all species seen to enter the tree and feed on fruits are recorded. At precise 5-min intervals, the number of individuals of each species present at that instant, the maximum number of individuals of each species present in the previous 5-min period, and the number of individuals of each species that were recorded feeding in the 5-min period are recorded. In addition the method by which the animals feeds on the fruits (and seeds) is noted to assess the likelihood of seed dispersal (versus seed or pulp predation). This method allows us to record the whole suite of potential seed dispersers for a given tree species their relative abundance and visitation frequency. This information, along with knowledge of their handling of the fruit and seed, is used to assess the relative effectiveness of the different fruit-eating animals.

Incidental observations of fruit-eating are all recorded and accumulated to supplement systematic observations from focal tree watches as well as animal follows (see below).

Data Collected: Over 2000 hours of focal observations have been conducted on over 16 species of trees; however, to date, our samples has been heavily biased towards particular species (such as Ekebergia capensis, Ficus oreodryadum, and Maesa lanceolata) to assess the response of particular seed dispersers.

4) Animal follows:

4A) Monkey Species: Follows of habituated groups of two species: Blue Monkey (Cercopithecus mitis) and Mountain Monkey (C. l'hoesti). (Kaplin, Munyaligoga) These species were chosen for study since they are the most abundant and widespread of the forest primates. The Blue Monkeys are known from previous studies to be potential seed dispersers. The Mountain Monkeys were very poorly known before this study and were thought to be of minor importance as fruit-eaters.

Methods: Monkey groups were habituated over a period of six months. Once habituated to the presence of a human observer, the group was followed 12 hrs per day for 4-7 consecutive days/month. During follows, two types of scans of all individuals in sight were performed every 15 minutes to determine activity budgets and diet. The scans included one 5 min scan of activity and three 3 min scans for diet. All movements were marked on maps. Vocalizations were recorded. All feces were collected for later analysis of seeds present (see method for fecal collection below).

Data Collected: Blue and Mountain Monkeys were observed from Jan 91 to Sep 91 and from Jan 92 to Aug 92. Blue Monkey follows resulted in 607 hrs in contact with the group and 512 hrs of scan data. Mountain Monkeys follows resulted in 574 hrs in contact with the group and 425 hrs of scan data.

4B) Large Canopy Birds: Follows of selected groups of three species of turacos: Black-billed Turaco (Tauraco shuetti), Ruwenzori Turaco (Musophaga johnstoni), and Great Blue Turaco (Corythaeola cristata). (Sun)

Method: Selected pairs or groups of turacos were followed by a team of three observers for 12 hr days with scans of activity taken every 3 min. The team of observers were able to coordinate their movements and observations to keep some individual turacos in view for all 3 min intervals for an entire 12 hr observation period! All feeding observations and social interactions were recorded as they were seen. The scan data were used to reconstruct diurnal and seasonal activity budgets.

Data collected: We have 14 months of animal follow data for all three species of birds. The total hours of observations are 475 hrs for Ruwenzori turaco (3 pairs were included in the study, each moth at least 2 pairs were observed), 434 hrs for Black-billed turaco (1 pair for some months only, a second pair for all 14 months), and 450 hrs for Great Blue turaco (1 group for only a few months, another group for all but 1 months).

5) Bird community study: Mist-netting of understory birds. (Kristensen)

Method: Three different 10 ha study sites were chosen to encompass a range of forest types: mature forest, natural forest edge, natural openings, road edge, and pine plantation. Within each site 14 0.1 ha circular plots were chosen for a total of 42 plots among the three sites. Each plot was scored according to physical and vegetation characteristics and assigned to one of the above "forest types". To census birds, one mist net (12m X 2.5m, 36mm mesh) was placed in each plot. 14 nets were operated at each site from 0600--1400 hrs each day for 2 consecutive days per month. All birds captured were identified, measured, weighed, and banded with individual 3 color band combinations and numbered aluminum bands.

Data collected: 906 individuals of 58 species were caught over a nine-month study period (Feb to Nov 91, excluding Jun). The data showed that even though species diversity was similar in all habitats (except the depauperate pine plantation), species composition, resident species composition, and age class distribution differ among sites. The results show that even after 20 years, selectively pitsawn logged areas differ from mature uncut forest in forest structure, tree species composition, and the character of the understory bird community.

6) Seed dispersal studies via fecal sample analysis:

6A) Primate fecal droppings, collection and analysis: (Kaplin)

Method: Fecal samples are collected only if the species source is known such as during direct follows of a species. Samples are washed and sieved to remove seeds which are then sorted for identification. A subset of seeds tested for germination to determine the effect of the monkeys on seed viability.

6B) Bird fecal droppings from mist-netted birds: (Kristensen)

Method: Birds caught in mist-nets typically defecate at the site of capture or within 15 min while

held in a soft, cotton bag (birds were held for measurement and banding). The feces from each bird are stored in small vials labeled according to the bird species, date of capture, site of capture, and specific net of capture. Later all seeds are removed from the feces, identified and counted. For each seed species present, minimum distances of seed-dispersal are estimated by measuring the straight-line distance between the mist net in which the bird was captured and the nearest reproductive individual of the seed species.

Data collected: Of 58 species of birds netted, 9 species were fruit-eaters. 161 fecal samples were collected from these 9 species. These samples contained seeds from at least 28 different species of plants, 23 of which were identifiable to genus or species.

7) Bird fruit handling/seed passage studies:

7A) Experimental aviary study of two bulbul species: Mountain Greenbul (Andropadus tephrolaemus) and Yellow-whiskered Greenbul (A. latirostris) (Graham, Moermond)

Method: Mist-netted birds were kept in 1m X 1m X .5 m cages and maintained on a special diet. Passage time was tested by feeding a subject 20 fruits of a given type. All fruits were eaten typically in one or two min after which the regular diet was returned to the bird and defecations were observed. We recorded time from ingestion of the fruit to defecation of the first seeds of that fruit. In separate trials, we noted the time of all subsequent defecations with seeds over the next hour or/alternatively, the total quantity of seeds defecated over each 20 min interval after ingestion.

Data collected: Six individuals of each species were used to generate multiple measures of each metric of passage time. The two species passed seed quickly (average time to first passage of 17.3 min for A. tephrolaemus and 12.3 min for A. latirostris). For both species virtually all seeds were defecated within 60 to 80 minutes of ingestion of the 20 fruits.

8. Analysis of fruit characteristics: (Sun, Kaplin, Kristensen)

Method: For plant with fruit eaten by at least one species of animal, the following characteristics were recorded: fruit type (e.g., berry, drupe, achene), fruit color when ripe, fruit size (length and width), fruit weight, seed number, seed size (length and width), and seed weight. Samples of seeds for each species were cleaned and dried and stored in sealed plastic bags to serve as a reference for identification of seeds found in animal feces.

Data collected: We measured the characteristics of ca 35 species of fruits collected in the forest throughout our field seasons. This includes the creation of a seed reference collection. In addition we have collected 17 species of fruits and 10 species of leaf samples for nutrient analyses.

II. SELECTED PRELIMINARY RESULTS:

The overall results in preparation will span several papers with more detailed description and justification of methods and data analyses. Here we would like to present some preliminary examples to give a more complete picture of the nature of the information being accumulated and its potential relevance to the stated objectives. The results will be grouped according to the organism

or method which was employed. The Figures (maps, graphs, and charts) are grouped at the end of this section in the order to which they are referred.

A. Study Site and Vegetation: Fig. 1 shows nearly 40 km of trails over the main portion of the study site (the Blue Site). Fig. 2 shows our preliminary map of vegetation types. Note both the diversity of vegetation types and the extreme mosaic they produce (the map includes the home ranges of the two species of monkeys studies which will be referred to below).

B. Phenology: Fig. 3 illustrates one combined index of the overall occurrence of flowers, ripe fruits, and young leaves over one year. Figs 4 shows an annual phenology for two different species of trees. Note the relative difference among the species in the timing and relative abundance of flowers (FLR), developing fruits (FF), unripe fruit (FI), and ripe fruit (FM).

C. Systematic Tree Observations: Of ten tree species with the largest data sets, we recorded a total of 29 species of birds and 3 species of mammals feeding on the trees. Despite marked differences among the trees in size, color, and type of fruit, overlap in list of visitors was large. Nevertheless, careful analysis of the relative frequency of visits of different fruit-eaters often showed much greater differences in the feeding patterns among trees as illustrated in Fig. 5 for Ekebergia capensis(EKCA) and Maesa lanceolata(MALA). Both trees had 17 visiter species recorded of which they shared 14. Nevertheless, when the proportion of observed visits by the species were compared, the differences in visitation patterns between the two trees are marked. Mammals (spp 1-3) and large birds (spp. 4-10) are more frequent on EKCA which has large fruits compared to the small fruits of MALA visited more heavily by small birds (bulbuls, spp. 17 and 19, and white-eyes, sp. 28).

D. Turaco Follows: The three species of turacos overlap significantly in their altitudinal range, Fig. 6 (Black-billed Turaco, left; Ruwenzori Turaco, center; Great Blue Turaco, right). The study took place in the zone of overlap between all three (2200-2500m). All three species are overwhelmingly frugivorous, eating a variety of primarily large-sized fruits. Fig. 7A illustrates their overlap in fruit diet (white circles show the number of fruit species eaten by each) and the percents show the number of those species shared with each other turaco. As in the two trees in Fig. 5, the overlap is considerably less when the relative quantity of the different fruit species is taken into account (Fig. 7B). Analysis of seasonal change in diet overlap between species relative to fruit availability is now in progress to target periods of potentially limited resources and food stress (Fig. 8).

E. Seed dispersal by small understory birds: Data from mist-netting and observations at focal tree watches identify two understory bulbuls, Andropadus tephrolaemus and A. latirostris, as probably the two most abundant fruit-eaters in the forest. Although they also overlap considerably in habitat and in diet, analysis of their seed dispersal distances (calculated from fecal samples taken from mist-netted birds, method 6B above) show marked differences in their median dispersal distances (Fig. 9). The differences correlate with observed differences in their social systems and associated movement patterns. Such differences are likely to bring significant differences in their importance as seed dispersers to the plant species illustrated.

F. Blue and Mountain Monkeys Follows: The two monkey species differ considerably in the size of their home ranges (see Fig 2) and in the average daily distance covered by a group (1.73km/day for Mountain Monkeys compared with 1.01km/day for Blues). The slower moving Blues spend

more time in tree canopies; while the Mountain Monkeys spend much more time on or near the ground (Fig. 10). Although the two monkey species also share many fruit species in common, they differ in the proportion of fruit and species of fruit in their diet (Fig. 11). Both monkey species eat fruits over a wide range of sizes and both show similar responses to differences in seed size (Fig. 12A). Germination viability trials with seeds recovered from dung samples, however, show that the monkeys differ in the degree of their effects on germination rates when compared eating the same species. Note, however, that despite that fact that both species ingest seeds of Beilschmidea, in both a certain portion of the seeds remain viable and hence a certain portion is likely successfully dispersed by the monkeys.

Although the monkey species differ dramatically in several respects, both appear to eat fruits frequently and, therefore, both are likely important seed dispersers for certain types of plants. One particularly interesting and valuable finding in this regard concerns the Mountain Monkey. This species, heretofore little studies, has a restricted range and is reportedly rare in most other localities and considered vulnerable to extinction. In the Nyungwe forest, not only is this species quite abundant, habitat use appears to favor open and disturbed sites within the forest mosaic (Fig. 13). Taking into account the patchiness of the habitat and the rapid rate of movement of this monkey species over a large portion of that habitat (Fig. 2), this species appears to be a prime candidate for movement of seeds from closed forest patches out into open habitats. This species, which is vulnerable and reduced to rarity in most remaining African natural forests (Oates 1985), may be one of the important agents of forest recolonization of open sites!

G. Conclusions:

1) A large portion of the trees of the Nyungwe forest are dispersed by animals. The degree to which they depend on animal dispersal for regeneration remains to be determined by future studies.

2) All tree species observed appear to be visited by several species of potential seed-dispersers. However, more quantitative observations are needed to determine the relative importance rank of those dispersers for each tree.

3) Although many of the animal species also overlap in the list of fruit species in their diets; the degree of overlap is less when relative consumption rates are included. Nevertheless, the importance of the overlap in times of food scarcity remains to be studied.

4) Several species of fruit-eaters can be identified as likely important tree seed dispersers:
a) Blue and Mountain Monkeys, b) Chimpanzees and Mangabeys, c) the turaco species, d) understory bulbuls, d) canopy starlings (Onychognathus spp. and Cinnyricinclus spp.), and Olive Pigeons (Columba arquatrix). No single method of study would identify these animals as important seed dispersers of tree seeds. Small understory birds may be particularly important in dispersing a wide variety of smaller fruited tree species.

5) Differences in movement patterns of different species suggest important differences in the consequences for plant dispersal. Seemingly significant differences even exits between congeneric species such as between the two Cercopithecus monkeys or between the two Andropadus bulbuls. This aspect will be examined in follow up studies.

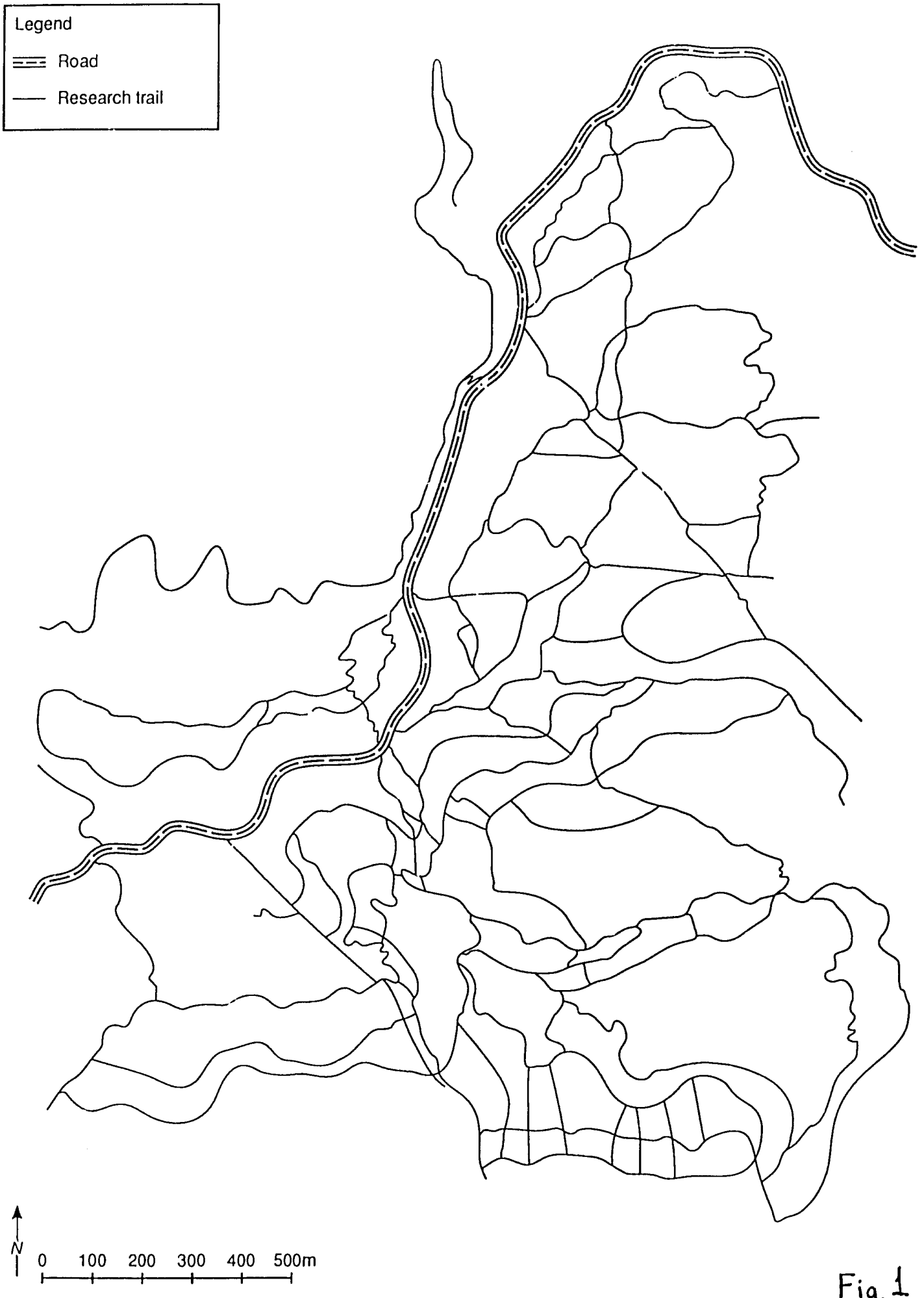


Fig. 1

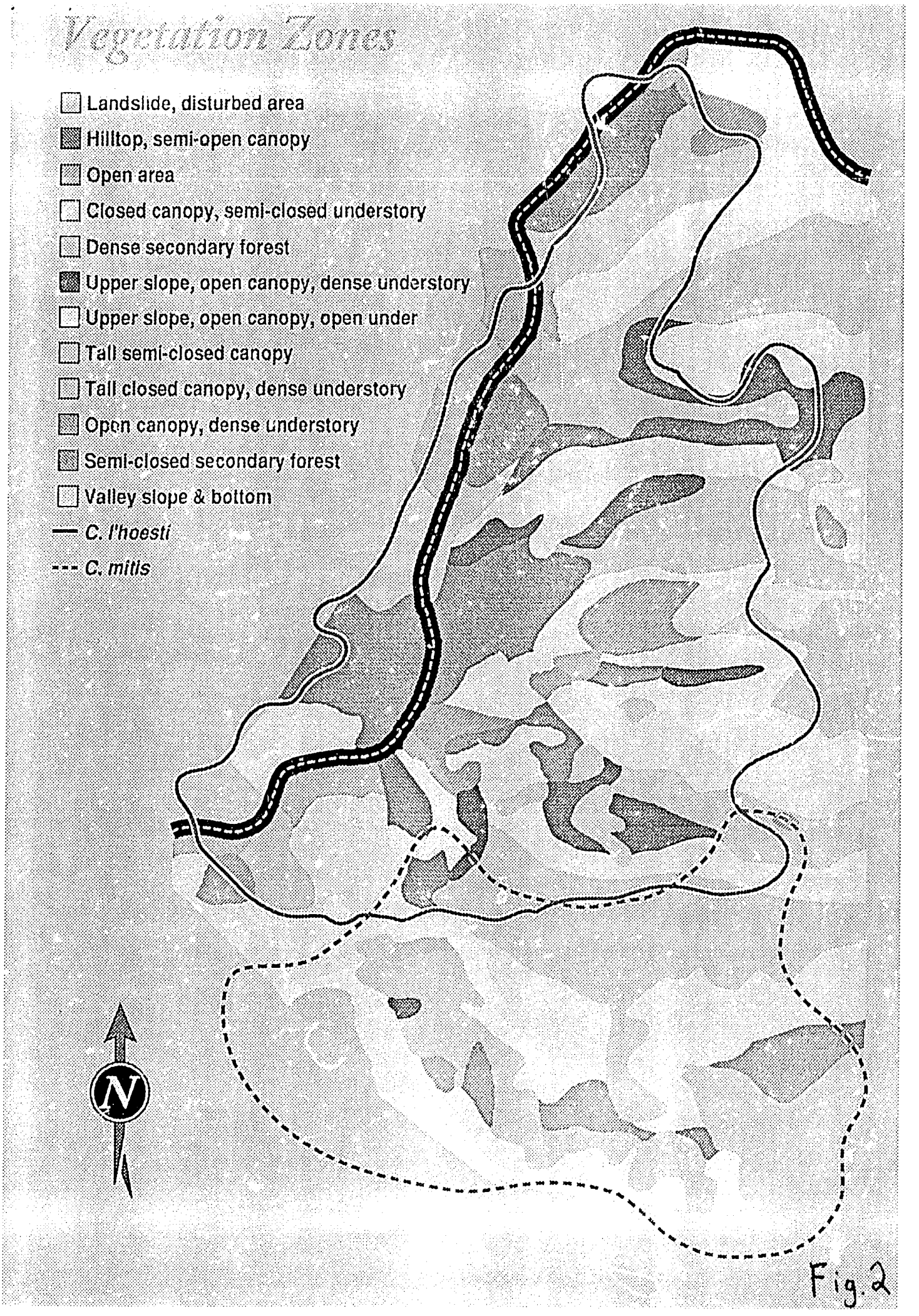

Vegetation Zones
Landslide, disturbed area
Hilltop, semi-open canopy
Open area
Closed canopy, semi-closed understory
Dense secondary forest
Upper slope, open canopy, dense understory
Upper slope, open canopy, open under
Tall semi-closed canopy
Tall closed canopy, dense understory
Open canopy, dense understory
Semi-closed secondary forest
Valley slope & bottom
C. l'hoesti
C. mitis
N

Fig. 2

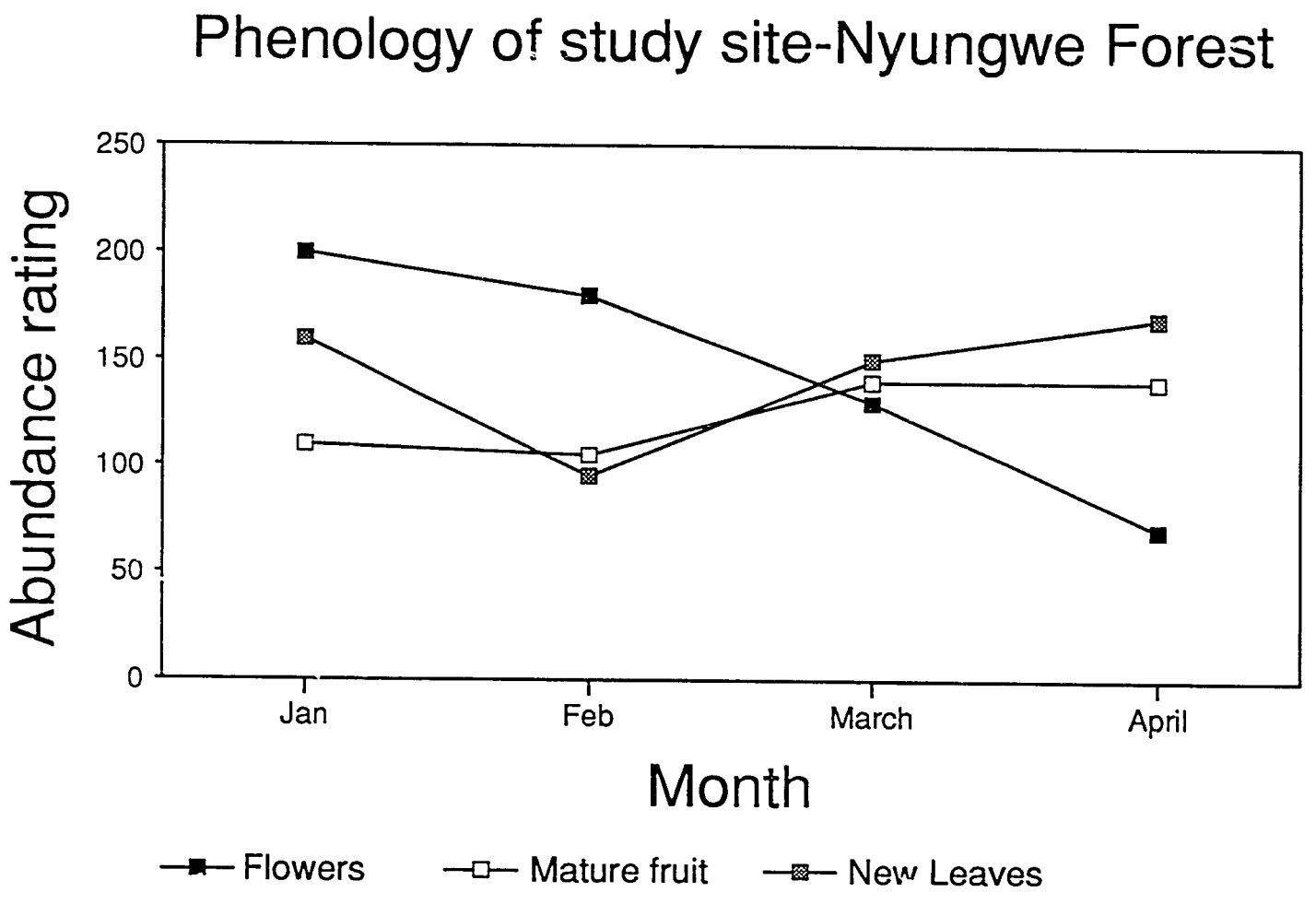
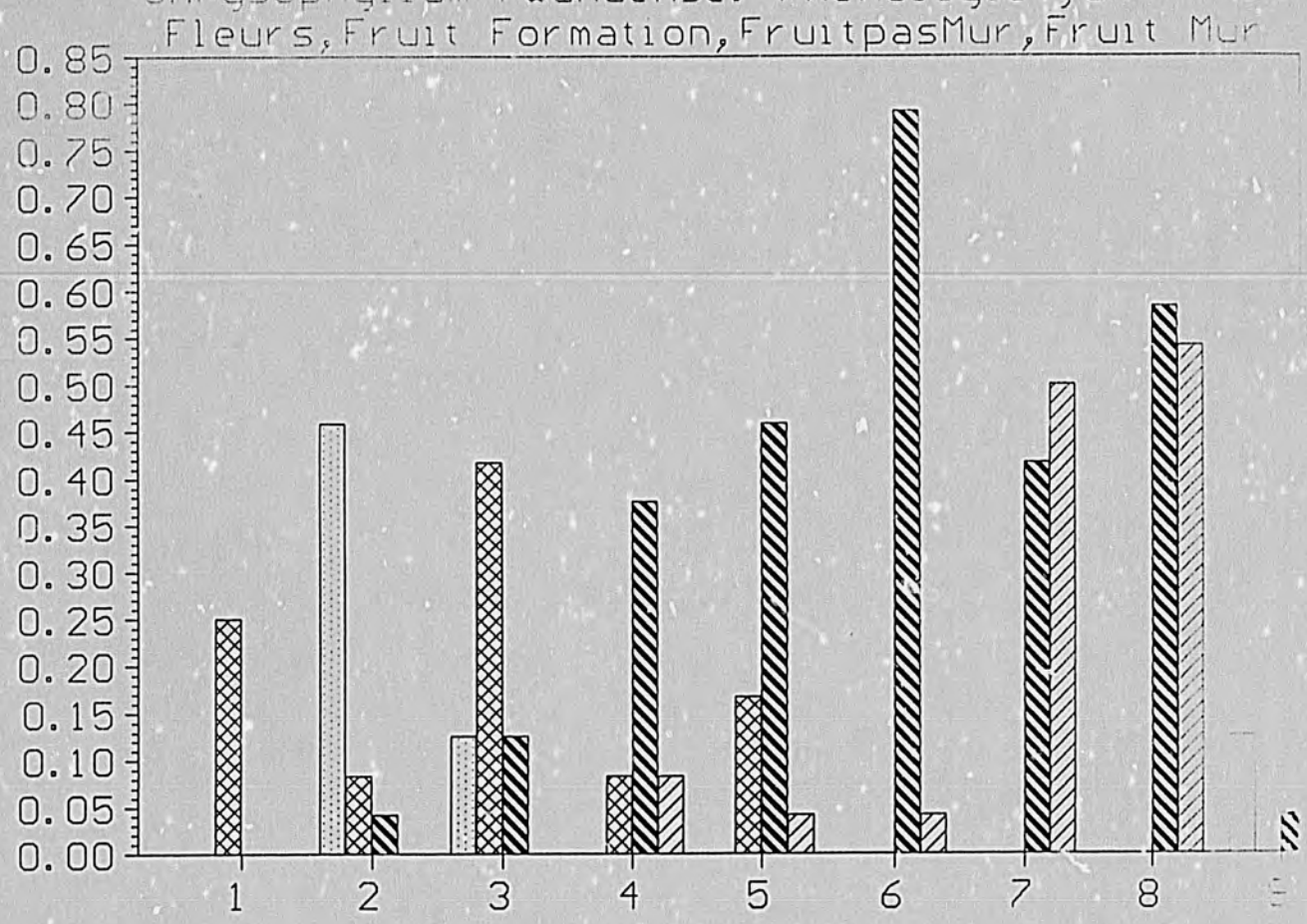

Phenology of study site-Nyungwe Forest
Abundance rating
250
200
150
100
50
0
Jan
Feb
March
April
Month
Flowers
Mature fruit
New Leaves

Fig. 3


Fleurs,Fruit Formation,FruitpasMur,Fruit Mur
0.85
0.80
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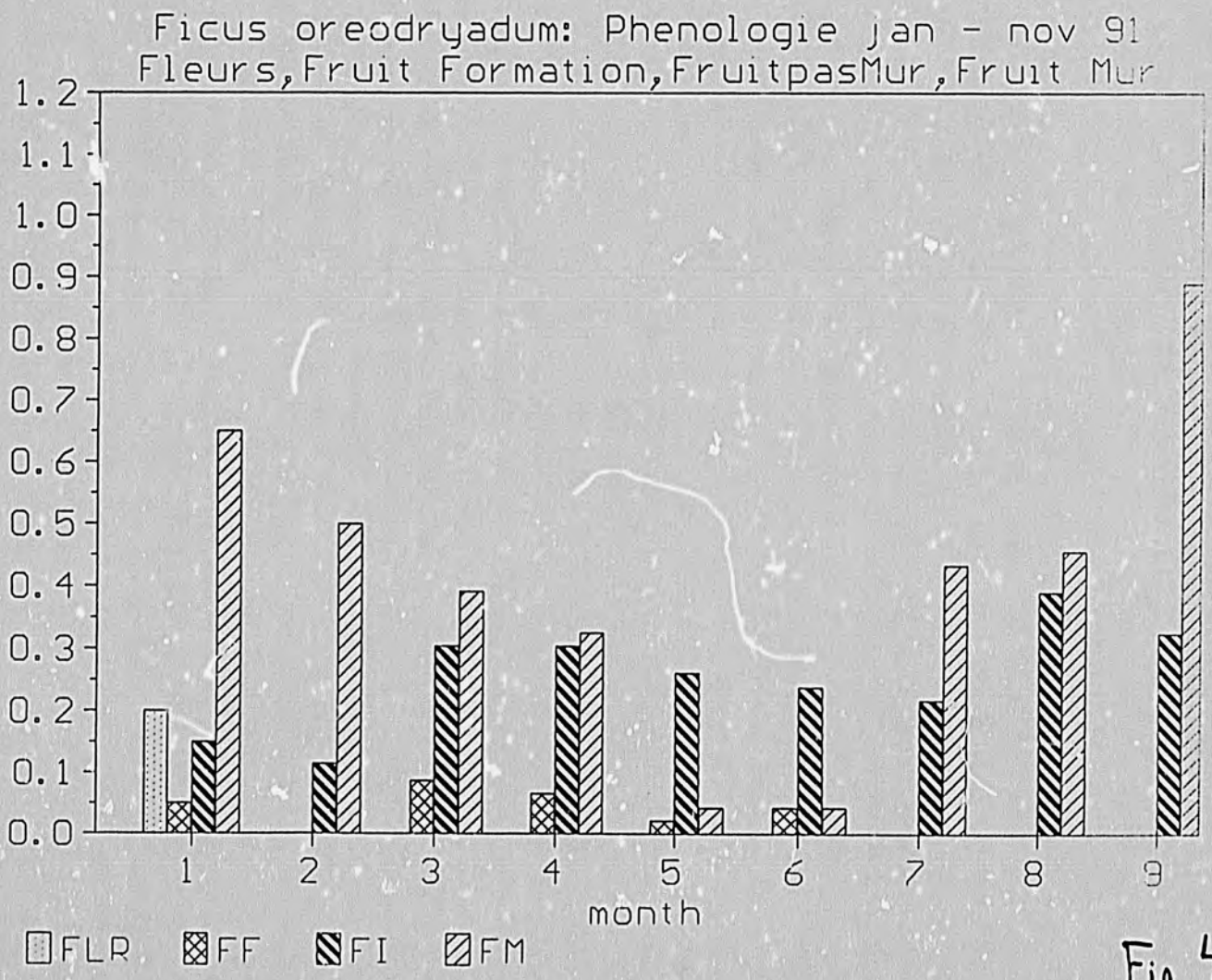
Ficus oreodryadum: Phenologie jan - nov 91
Fleurs,Fruit Formation,FruitpasMur,Fruit Mur
1.2
1.1
1.0
0.9
0.8
0.7
0.6
0.5
0.4
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Fig. 4

Figure 1

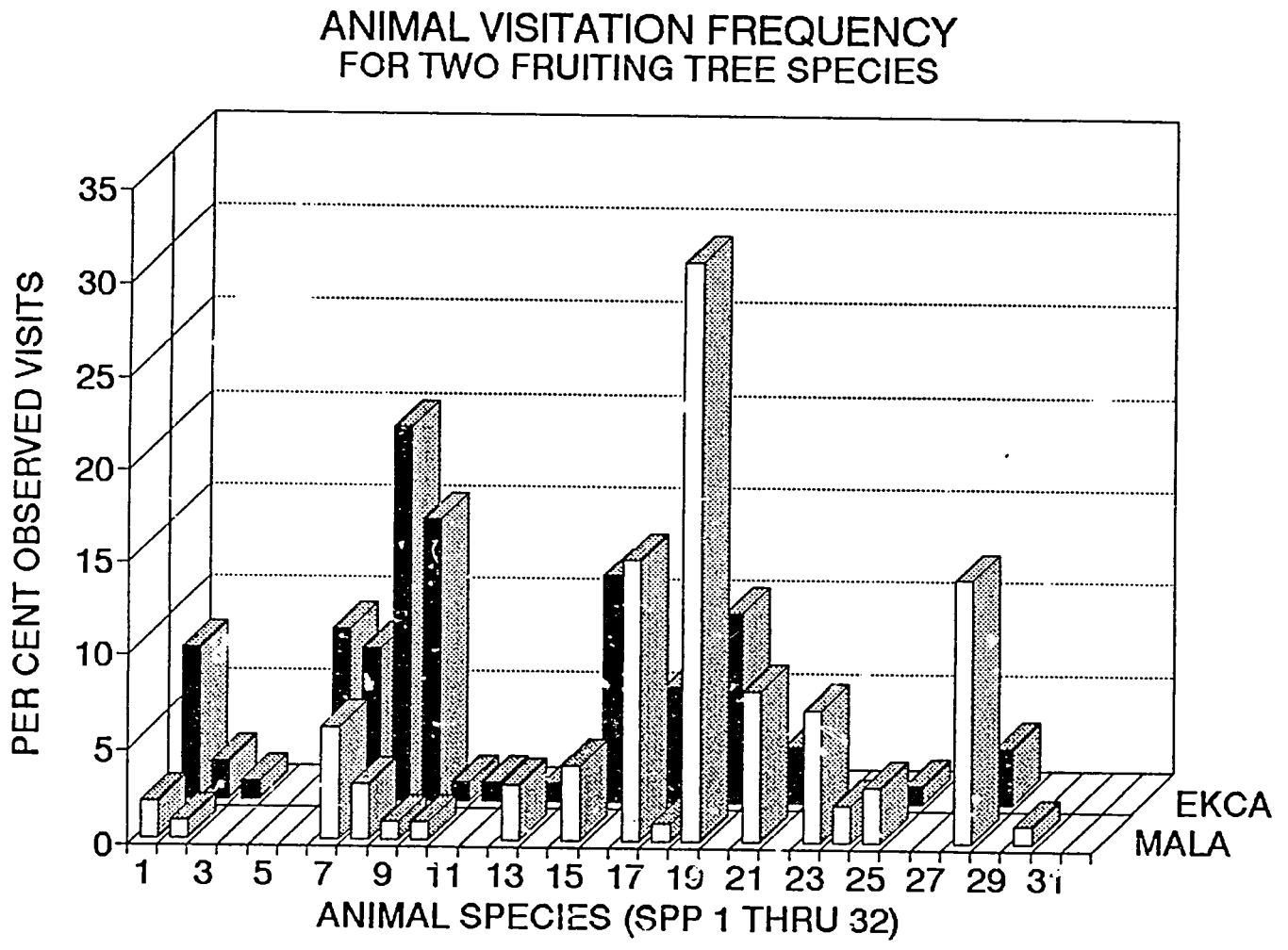
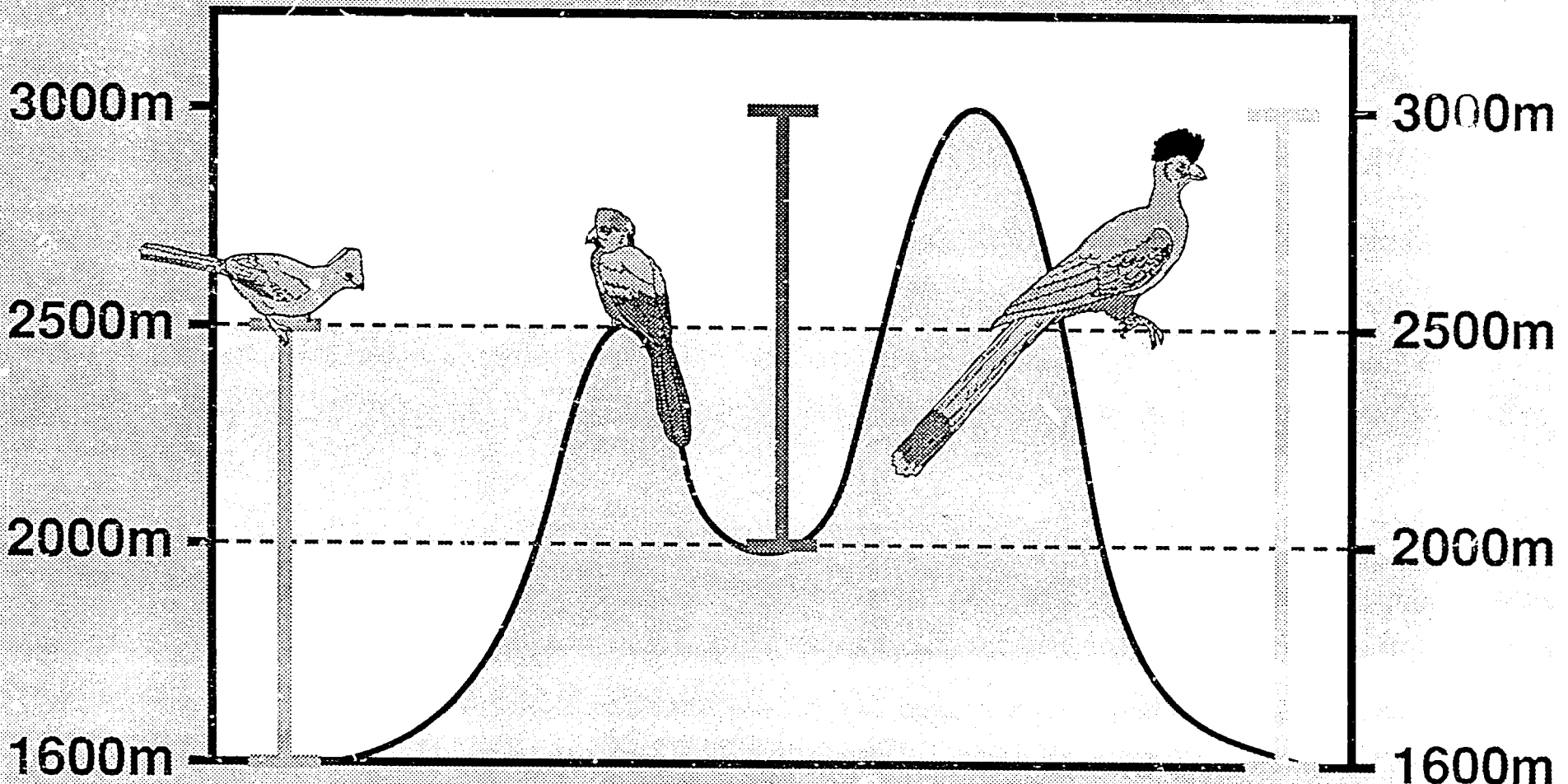


Fig. 5



Altitudinal Distribution of Turacos

Fig. 6

Percentage of Food Items Overlap
(All Items Treated Equally)

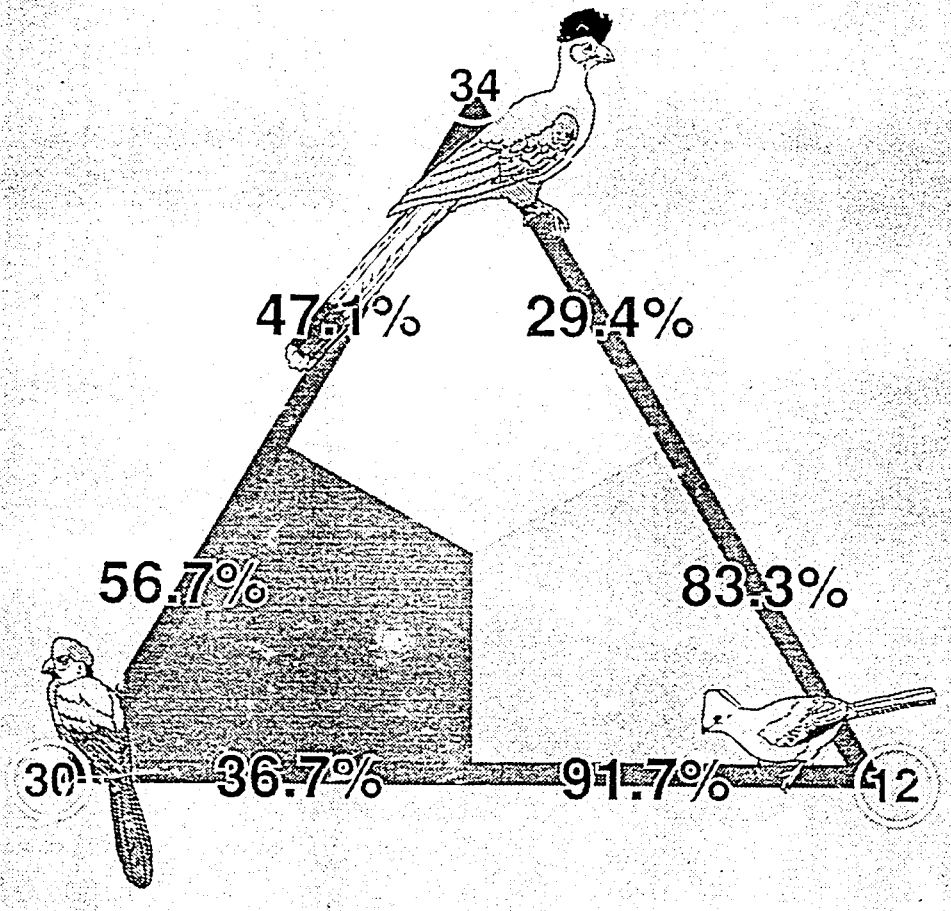


Fig. 7 A

Schoener Overlap Index
(Percentage Overlap)

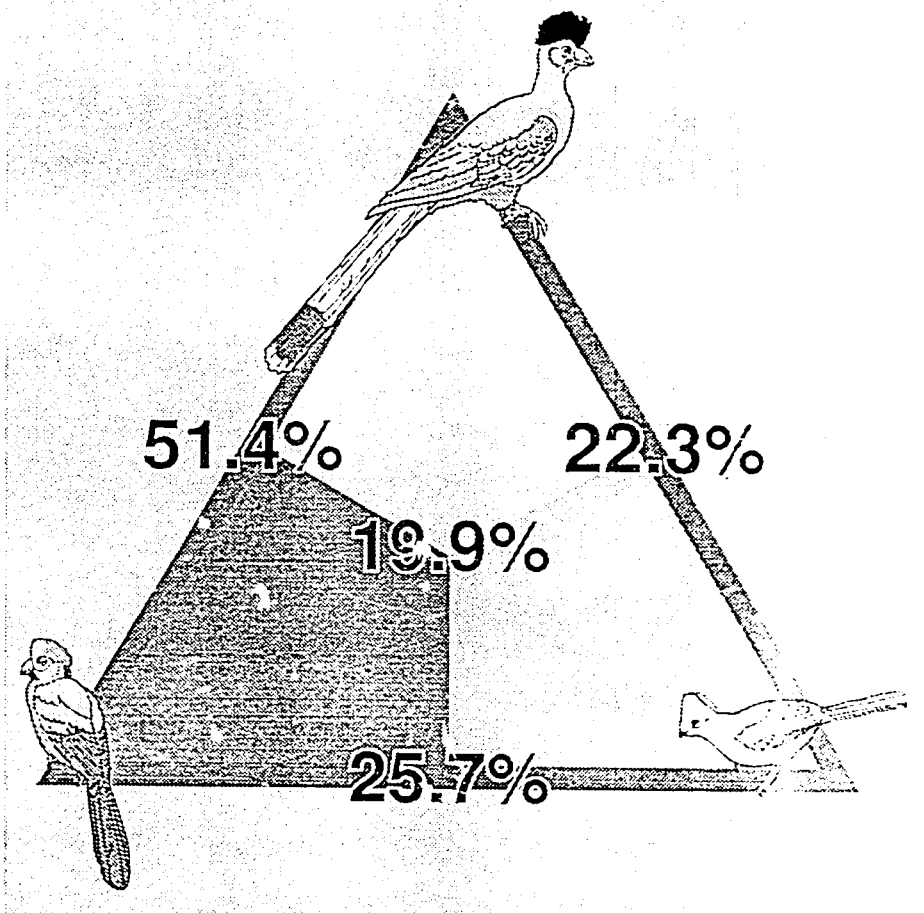


Fig. 7 B

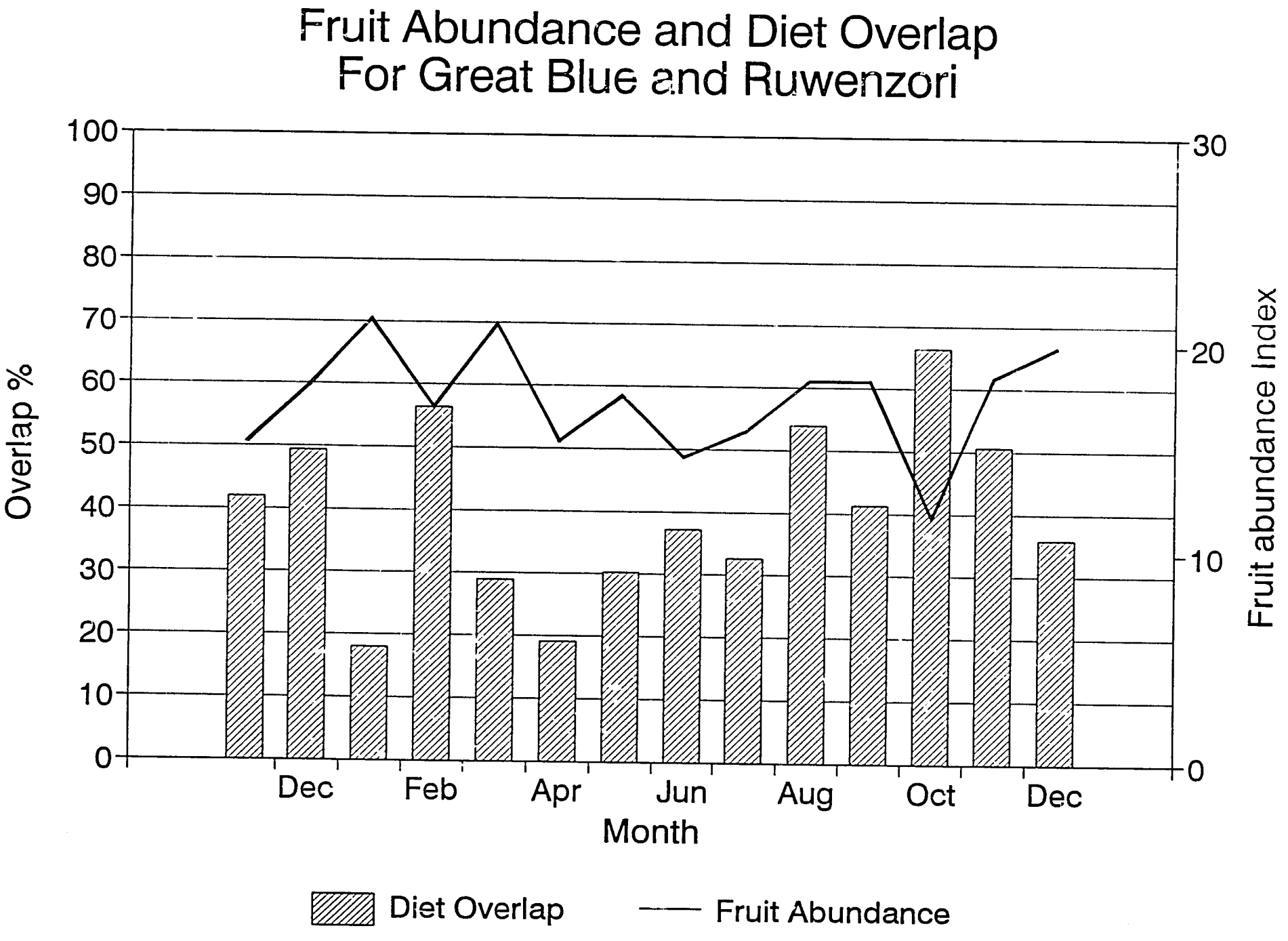
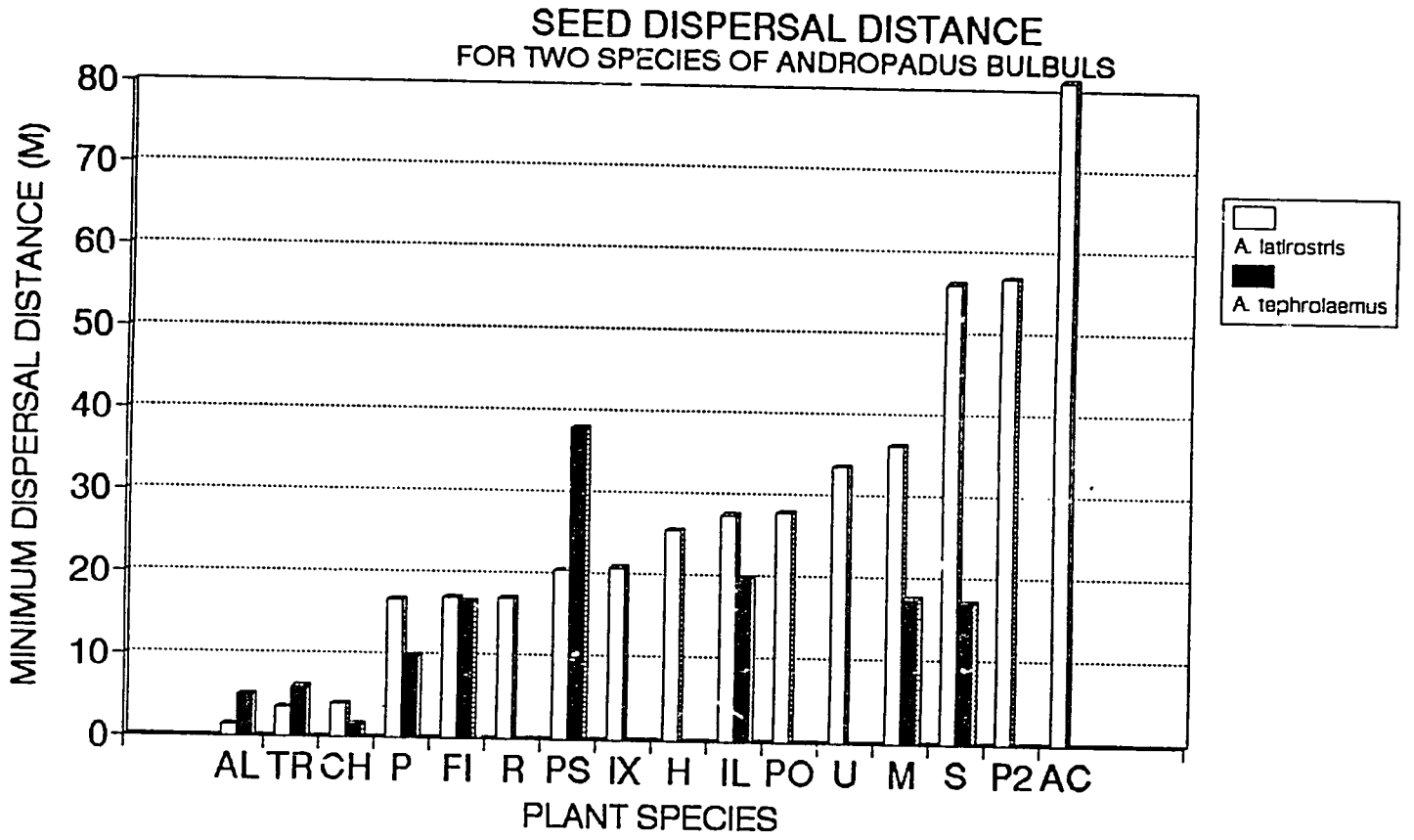

Fruit Abundance and Diet Overlap
For Great Blue and Ruwenzori
Overlap %
100
90
80
70
60
50
40
30
20
10
0
Fruit abundance Index
30
20
10
0
Dec
Feb
Apr
Jun
Aug
Oct
Dec
Month
Diet Overlap
Fruit Abundance

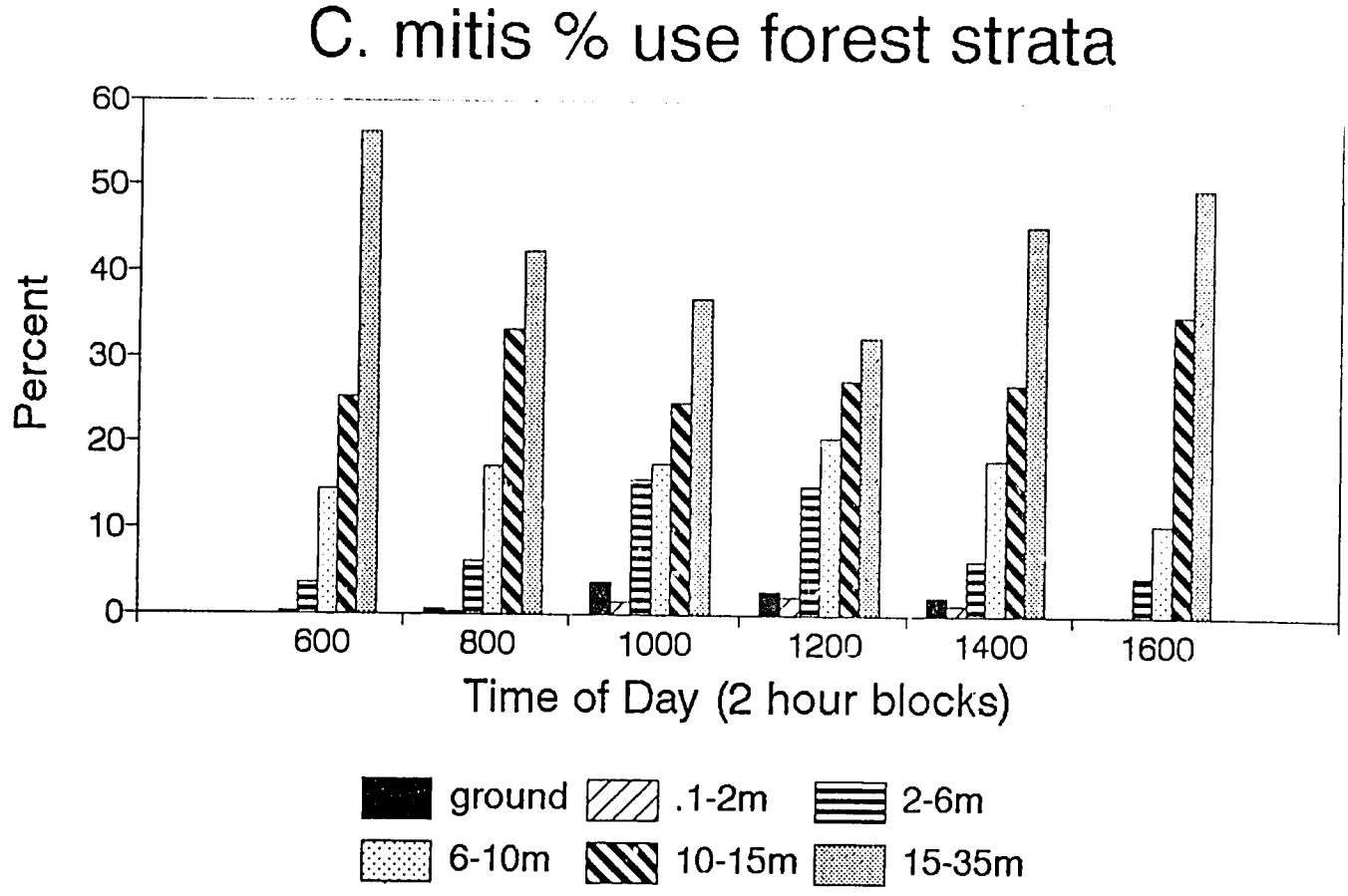
Fig. 8

Figure 9



AL Allophylus spp.; TR Tricalysia spp.; CH Chassalia subchreata; P Prunus africana (excluding 2 records of 500 m dispersal events) FI Ficus oreobatum; R Rubus spp.; PS Psychotria mahonni; IX Ixora burendensis; H Harungana montana; IL Ilex mitis PO Polyscias Fulva; U Urera hypseldon; M Maesa lanceolata; S Schefflera goetzenii; P2 P. africana (including 2 records of 500m dispersal events); AC Alangium chinensis

Fig. 9


C. mitis % use forest strata
Percent
60
50
40
30
20
10
0
600
800
1000
1200
1400
1600
Time of Day (2 hour blocks)
ground
.1-2m
2-6m
6-10m
10-15m
15-35m

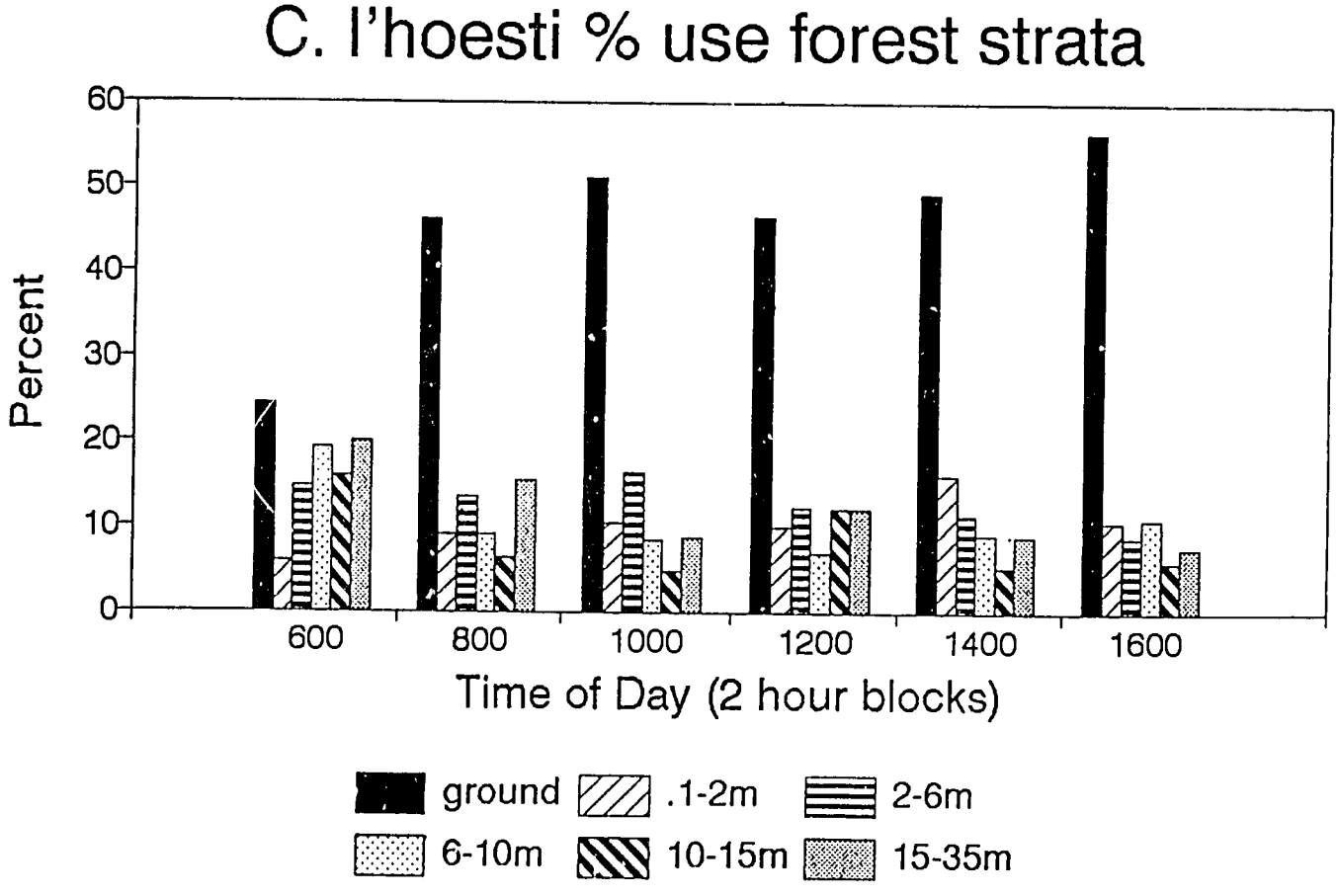

C. l'hoesti % use forest strata
Percent
60
50
40
30
20
10
0
600
800
1000
1200
1400
1600
Time of Day (2 hour blocks)
ground
.1-2m
2-6m
6-10m
10-15m
15-35m

Fig. 10

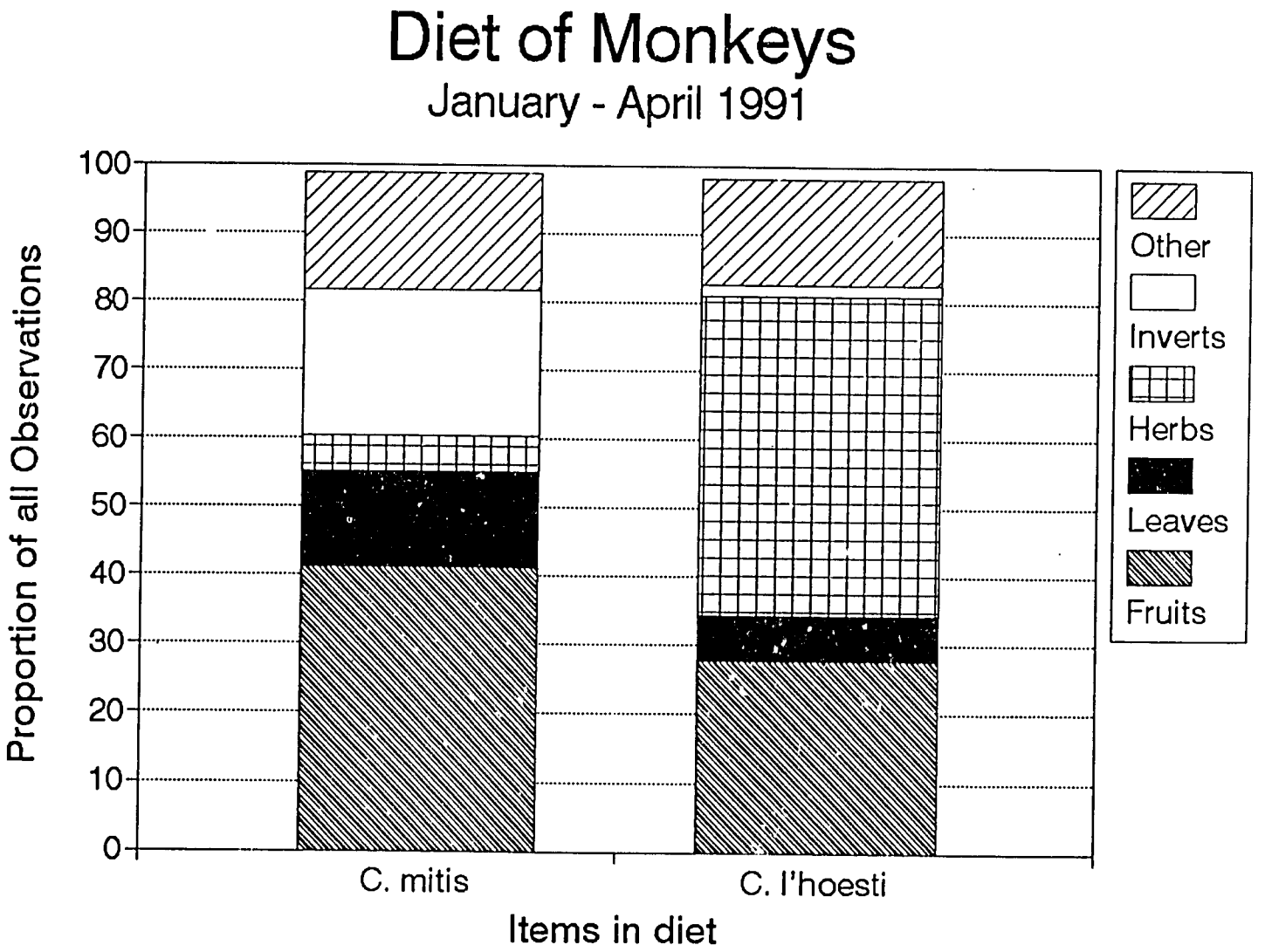

Diet of Monkeys
January - April 1991
Proportion of all Observations
100
90
80
70
60
50
40
30
20
10
0
C. mitis
C. l'hoesti
Items in diet
Other
Inverts
Herbs
Leaves
Fruits

Fig. 11

A. MODES OF SEED HANDLING
C. L'HOESTI & C. MITIS

Tree or Shrub Spp.	Seed #	Seed diam. (mm)	L'hoesti def	L'hoesti drop	L'hoesti eat	Mitis def	Mitis drop	Mitis eat
Parinari excelsa	1	60					x	
Chrysophylum rwandense	1	25	x*	x		x*	x	x
Beilschmidea troupinii	1	20		x	x		x	x
Strombosia shefflera	1	20		x	x		x	x
Rytiginea kiwuensis	2	10		x			x	
Alchornea hirtella	3	3			x			x
Macaranga neomild.	1	3	x*		x	x*		x
Psychotria mahonii	2	3	x			x		
Chassalia subochreata	2	2	x			x		
Harungana montana	5	2	x			x		
Ilex mitis	4-6	1	x			x		
Balthasarea schliebenii	many	1	x			x		
Ficus oreodryatum	many	1	x			x		

B. GERMINATION TEST RESULTS
PULP REMOVED & SEEDS SPIT OUT BY MONKEYS

	SEED SPECIES	SAMPLE SIZE	% GERMINATION
C. l'hoesti	*Beilschmidea*	*27*	*30%*
C. mitis	*Beilschmidea*	*73*	*52%*
C. l'hoesti	*Chrysophylum*	*39*	*23%*
C. mitis	*Chrysophylum*	*14*	*36%*

Fig. 12

Figure13

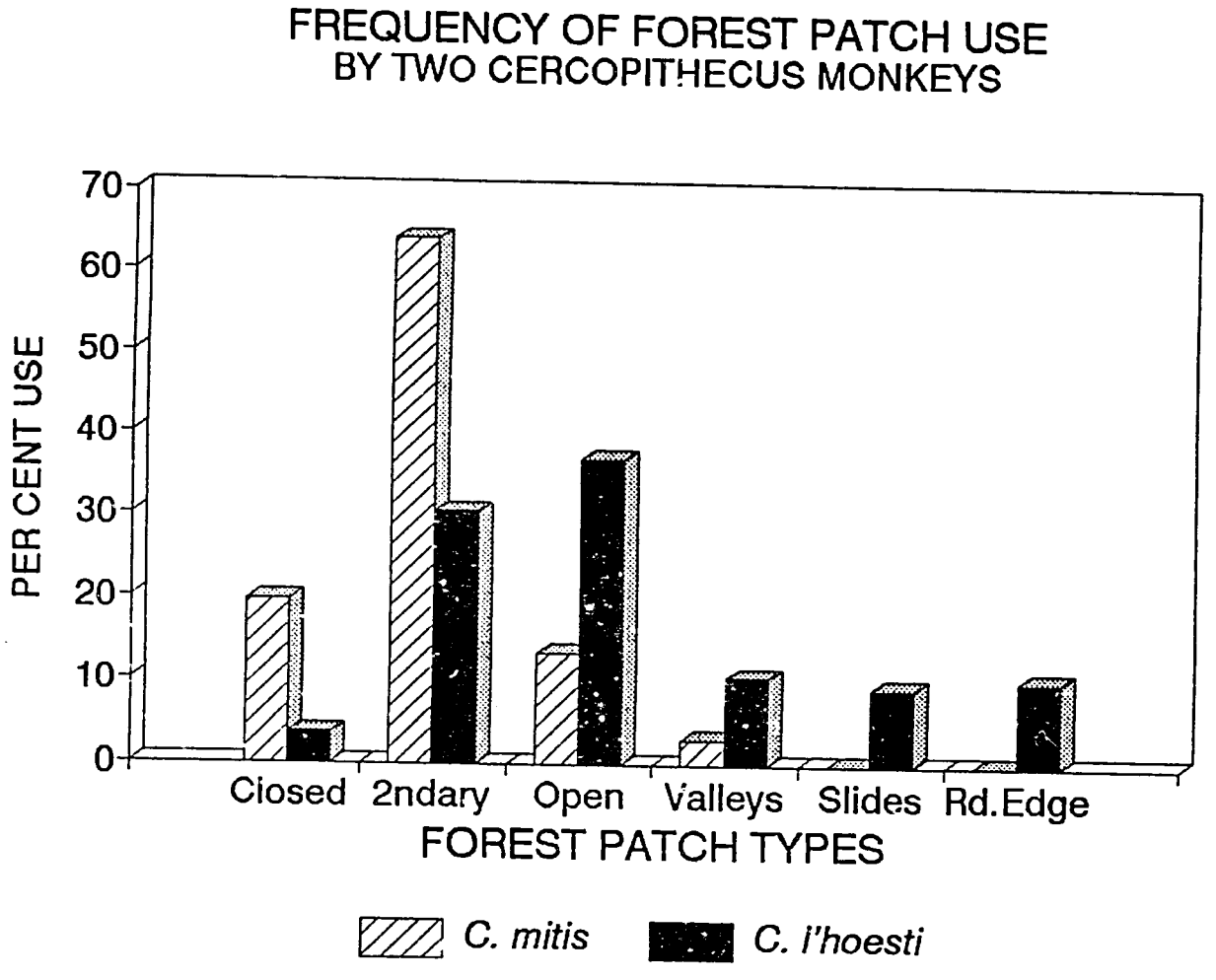


Fig. 13

IMPACT, RELEVANCE AND TECHNOLOGY TRANSFER

I. TROPICAL FOREST CONSERVATION AND MANAGEMENT

The site of the project is the species-rich Nyungwe Forest in Rwanda, central Africa. This forest is one of the largest (90,000 ha) and most ecologically diverse lower montane forests in central Africa (Sorg 1978, Storz 1982, Weber 1987). With 13 species of primates (Oates 1985) and 17 of its 275 birds species endemic to the Kivu region (Prigogine 1985), Nyungwe has been placed on several lists in the highest priority category for conservation (Collar and Stuart 1988, IUCN 1986).

Rwanda, has an average of 300 people per km^2, the highest population density in Africa. The pressing needs of Rwanda require that most or all ecosystems provide economic returns (Vedder 1987). Although approximately 30% of the country's 26,338 km^2 may have been forested at one time, today approximately 5% remains in natural forest (Vedder 1987). The value of forest for watershed protection, for selective timber production, and for diverse biological resources is recognized (Budowski 1976, Sorg 1978, Vedder 1987). The critical challenge for this and other tropical forests is to find ways that they can be managed that benefit local people while maintaining their high irreplaceable biological diversity of these forests (Anderson 1990, Goodland 1990, Okapi 1992, Panayotou and Ashton 1992).

The science of managing tropical forests is far from adequate to meet this challenge (see Gomez-Pompa et al., 1991, for a recent assessment). Recent attempts to outline sustainable ecological approaches to tropical forestry (Poore and Sayer 1991, Panayotou and Ashton 1992) fail to incorporate fruit-dispersers as key elements to maintain forest dynamics and composition. A recent statement of research needs speaks directly to this challenge (Swaine 1989): "The future of tropical forests...depends particularly on developing sustainable yield management methods which can predict the consequences for floristic composition of various exploitation practices. Foresters need the help of ecologists and botanists to link more closely the processes of logging and regeneration."

The process of natural regeneration of these forests depends on a basic set of processes: seed production, seed dispersal, seedling establishment, and survival of seedlings to reproductive adults (Janzen and Vasquez-Yanes 1991). Establishment involves finding a suitable site with necessary soil and microclimatic conditions for seed germination and growth. Successful reproduction depends very strongly on seed dispersal to allow seeds to be removed from the vicinity of a parent tree where they escape the high seed mortality present close to the parent plant (Janzen 1970, Howe and Smallwood 1982, Howe 1992) and to find suitable sites for germination and establishment.

A very high proportion of tropical trees and shrubs depend on animal fruit-eaters, particularly birds and primates, for seed dispersal (Gentry 1982, Stiles 1985). The predominance of these animals as dispersers suggests a major role in the natural dynamics and maintenance of diversity in tropical forests (Gentry 1982, Howe and Smallwood 1982, Terborgh 1986, Howe and Westley 1988, Gautier-Hion et al. 1985, Stiles 1985, Moermond and Denslow 1985, Estrada and Fleming 1986). Several studies have documented potential value of animal seed-dispersers as agents of reforestation, enhancing both the rapidity and diversity of natural regeneration (Debussche et al. 1982, McDonnell and Stiles 1983, Guevara and Van der Maarel 1986, Campbell et al. 1990, Nepstad et al. 1990, McClanahan and Wolfe 1992). The presence of such dispersers, however, may be significantly

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altered by human exploitation of natural forests. A few studies have become to document the vulnerability of animal seed dispersers to human disturbance of forest (Skorupa 1986, Johns 1992, Thiollay 1992).

To maintain both the regeneration patterns of natural forests as well as that of economically important tree species, it is essential to retain dispersers in the system. The study of seed-dispersal is highly relevant to the future management of tropical forests as patterns found in seed dispersal mechanisms can lead to manipulation of species composition to compensate for the impacts of selective logging to maintain natural patterns of vegetation dynamics or to enhance the economic value of the forests (Bawa et al. 1989).

This study now has collected data and ecological insights to extend the knowledge base about the animal seed dispersal/tree regeneration interaction, particularly so with regard to previously little studies African forests. In addition this study has involved collaborative activities in training and institution building to enhance the likelihood that the results and perspectives generated by this project will influence future management plans for natural forests in Rwanda.

II. INSTITUTION STRENGTHENING

Collaboration and Training:

The projet has increased the potential for further conservation concepts, research, and application in Rwanda. The project has involved extensive collaboration with several African researchers (see above under "The Research Team"). Each of them was recruited to the project on the basis of their interest, their qualification, and expertise. All of them are concerned with conservation of their country's rich biological diversity and all are in positions to promote further conservation research and actions within their country. The study is the first of its kind in Rwanda that incorporates new concepts, approaches, and techniques of conservation of natural biological diversity into a cadre of young Rwandan researchers including Rwandan university students. Several of them are involved with research or management of the Nyungwe Forest and are in excellent positions to apply principles arising from the proposed study.

This project began officially as a subproject of the Project for the Conservation of Nyungwe Forest (funded by the AID-Mission to Rwanda and the Wildlife Conservation Society) under the auspices of the Office Rwandais de Turisme et Parcs Nationaux (ORTPN). As the collaboration with Rwandan researchers developed and strengthened, the project was shifted to the Institut de Recherche Scientifique et Technologique (IRST). This move was initiated by Joseph Mvukiyumwami and facilitated by the Director General of the IRST, Francois Gasengayire, to strengthen the research of the IRST directed toward the conservation of biodiversity. The IRST has been designated as an important Rwandan resource for environmental research and as the mechanism to coordinate multi-disciplinary research efforts involving collaboration of other institutions. The IRST facilitated a further official research collaboration between the project and the Institut des Sciences Agronomiques Rwandais. This convention will allow the major participation in the future planned work of their head of research on natural forests, Isaac Kabera. Kabera played a substantial role in planning the new research effort at the site (see Future Work) and will also be funded by the project for Ph.D. work at the University of Wisconsin-Madison.

Strengthening of infrastructure for natural forest research:

Research base: The nature and design of the work at the Uwinka field site contributes to a valuable base for future research efforts on the ecology and management of natural forests in Rwanda. The following elements are illustrative: 1) mapped trail system: we have established a 50 km network of marked trials facilitating field work on flora and fauna in that area (the steep topography of the Nyungwe forest discourages or prevents work outside a trail system), 2) the detailed vegetation map with the large set of permanently marked plots, 3) the long-term monthly tree phenology record, 4) the daily rainfall/temperature data), and 5) the habituated groups of animals. All these provide a valuable base on which to begin new studies of many types.

Field technician staff: In addition, Sun, Kaplin, and Kristensen have recruited and trained 8 local workers who have developed into an skilled reliable team of field technicians who are extremely knowledgeable of the local flora and fauna (knowing identification characteristics and scientific names) and who have experience in a variety of ecological techniques and data collection procedures. This team forms a valuable field staff core to support future field study efforts of Rwandan researchers at the site. [They also have become a group knowledgeable about conservation perspectives and, as a result, "good-will ambassadors" in the local community at the forest edge.]

Permanent logistic base: Through the collaboration with IRST researchers, we are now seeking funds to establish a permanent base for this and related research on the Nyungwe forest. This and related developments arising from the success of the project will promote the growth of Rwandan research on conservation of biodiversity and its application to sustainable management of Rwandan natural forest resources.

PROJECT ACTIVITIES/OUTPUTS

I. PRESENTATIONS:

Formal presentation of results at national and international professional meetings (listed under each meeting by principal author and title of the presentation).

2ND INTERNATIONAL WORKSHOP AND SYMPOSIUM ON FRUGIVORY AND SEED DISPERSAL, CATAMACA, MEXICO, JUNE, 1991

Kaplin et al. Frugivory and seed-dispersal of Cercopithecus l'hoesti and C. mitis in Nyungwe forest, a tropical montane forest in Rwanda, central Africa.

SOCIETY OF CONSERVATION BIOLOGY MEETING, MADISON, WI, JUNE, 1991

Kaplin et al. Ecology and seed dispersal of Cercopithecus l'hoesti and C. mitis in Nyungwe forest, Rwanda: Implications for tropical forest conservation.

Kristensen et al. The effects of forest disruptions upon the understory frugivorous birds, seed dispersal, and possible consequences for natural regeneration in the Nyungwe forest, Rwanda.

Moermond et al. Animal seed-dispersers as key elements for conservation of the Nyungwe forest of Rwanda, Africa.

FLORIDA ACADEMY OF SCIENCES, 1992

Graham, C. Seed dispersal by two bulbuls on Maesa lanceolata, an African montane forest tree. (Award for best student paper)

8TH PAN AFRICAN ORNITHOLOGY CONGRESS, BUJUMBURA, BURUNDI, OCT, 1992

Sun et al. The comparative ecology of three sympatric species of turacos in a montane forest of Rwanda.

Moermond et al. Avian frugivory in a montane rain forest: tree visitation patterns.

ECOLOGICAL SOCIETY OF AMERICA MEETING, MADISON, WI, JUNE, 1993

Kaplin et al. Seed dispersal by two species of African monkeys: potential for regeneration of human-disturbed forest.

Sun et al. The comparative ecology of three sympatric species of turacos in an African rain forest.

Kristensen et al. Seed dispersal by understory fruit-eating birds in an Afromontane forest.

II. PUBLICATIONS:

Moermond, T.C., K. ka Kajondo, C. Sun, K. Kristensen, V. Munyaligoga, B.A. Kaplin, C. Graham, and J. Mvukiyumwami. 1993. Avian frugivory in a montane rain forest: tree visitation patterns. Pp. 421-428. In: T. Wilson (ed), Proceedings of the Eighth Pan-African Ornithological Congress: Birds and the Environment, Annales Sciences Zoologiques No. 268, Musee Royal de l'Afrique Centrale, Tervuren, Belgium.

III. THESES COMPLETED:

Graham, C. 1992. Frugivory and Seed dispersal by two bulbuls on Maesa lanceolata, an African montane forest tree. Senior Honors Thesis, Eckerd College, St. Petersburg, Florida.

Munyaligoga, V. 1992. Activity and Diet of Blue Monkeys in the Nyungwe Forest, a Preliminary Study. License Memoire, Universite Nationale du Rwanda, Butare, Rwanda.

Kristensen, K.A. 1993. Human Disturbance and Seed Dispersal by Understory Avian Frugivores: Key Elements in the Maintenance of Tropical Forest Diversity. Master of Science Thesis, University of Wisconsin-Madison, Madison, Wisconsin.

IV. MANUSCRIPTS COMPLETED:

Graham, C., T.C. Moermond, K.A. Kristensen, and J. Mvukiyumwami. Seed dispersal effectiveness by two bulbuls on Maesa lanceolata, an African montane forest tree. Ecology, under review.

Kristensen, K.A., T.C. Moermond, and J. Mvukiyumwami. Seed dispersal distances by African forest understory birds. to be submitted to Biotropica.

Kristensen, K.A., and T.C. Moermond. African forest birds and human disturbance: effects of roads, pitsaw logging, and pine plantations. to be submitted to Biological Conservation.

V. MANUSCRIPTS IN PREPARATION:

The following manuscripts are planned. Some are in the process of being written. For most, data analysis is still in progress. The manuscripts are grouped under the author principally responsible for publication.

A. Beth Kaplin, et al.

1) Variations in fruit availability and feeding behavior in one group of Blue monkeys, Cercopithecus mitis doggetti.
2) Activity patterns and ranging behavior in one group of Blue monkeys, Cercopithecus mitis doggetti.
3) Diet in one group of Mountain monkeys, Cercopithecus l'hoesti.
4) A comparison and discussion of methods for observing and recording monkey diets in dense tropical forests.
5) Vegetation communities within a human-disturbed tropical forest: patterns of abundance, density, and regeneration.
6) Seed dispersal by two species of Cercopithecus monkeys in a montane tropical rain forest.
7) Meat-eating by Cercopithecus mitis doggetti in Nyungwe Forest, Rwanda.

B. Chin Sun et al.

1) The phenology of a tropical montane rain forest in Rwanda, Africa
2) The comparative ecology of three sympatric species of turacos in an African rain forest
3) Seed dispersal by three species of African forest turacos.
4) Seasonal change in territorial behavior of two tropical turaco species.
5) New practical field method for direct visual monitoring of African forest turacos.

C. Moermond et al.

1) Animal seed dispersers as key elements in a process-oriented approach to tropical forest conservation.
2) Contrasts in perch use ability by 2 bulbul species.

PROJECT PRODUCTIVITY

The project went far beyond our expectations. 1) We have amassed an incredible quantity of interesting and relevant data (including some of the best studies ever assembled for particular species such as the Mountain Monkey (Cercopithecus l'hoesti) and the three turaco species), 2) we have developed a strong collaboration with researchers and their institutions in Rwanda which has resulted in an even more extensive input from Rwandan researchers in design and plans for implementation of our future work, and 3) we have gained new insights into the animal seed-dispersers/tree regeneration dynamics which promises to offer a substantial basis for natural forest management and new innovative manipulative methods for enhancing forest restoration in degraded habitats.

FUTURE WORK

Two complementary proposals for future work in Rwanda to build on results of this project have recently been approved for funding. The scientific summaries and/or statements of scientific objectives of each are provided below.

II. NEW AID/PSTC PROPOSED WORK:

Title: Seed-Dispersal and Vegetation Dynamics in a Human-Disturbed Tropical Forest.

The understanding and new perspectives gained from the three years of the project have resulted in the development of a new proposal for a follow-on project at the same site. This proposal (no. 13.342) received a strong review and was approved for funding, starting in September, 1993, for three years. The following sections of the proposal are appended to highlight the direction, objectives, and expected benefits of this new study. This new study is based on novel ideas which were derived from the work of the project reported on here.

Scientific Summary:

The interaction of animal seed-dispersal and forest regeneration dynamics within human-disturbed areas will be studied in the Nyungwe Forest in Rwanda, central Africa. Fruit-eating species of birds and monkeys have been shown to be primary dispersers of seeds of the majority of forest tree and shrub species. However, little is known of the spatial patterns of seed-dispersal, of how such patterns are affected by the activities of animal dispersers, and of how the animals are influenced by elements of the forest habitat mosaic.

We will investigate how selected components of the plant animal seed-disperser interaction affect regeneration dynamics in a tropical forest. We will focus on these animals and the transport of seeds from closed forest patches into natural and human-disturbed areas such as secondary forest patches and forest clearings. Movement of fruit-eating animals into these disturbed or altered forest patches may have significant effects on vegetation regeneration in these areas.

The diversity and actions of animal fruit-eaters entering these disturbed forest patches will be determined with data from focal tree watches and direct animal follows. Animal movements and

associated seed transport will be monitored relative to elements and characteristics of disturbed patches. These elements will include sites such as open areas versus edge and specific trees of non-fruiting species and of fruiting species in different stages of the fruiting cycle. The consequences of differential visitation patterns among these elements will be assessed by comparison of sequential stages in the seed-dispersal/tree regeneration process. This will entail systematic measurement of i) species and quantities of seeds entering selected patches (seed rain), ii) species composition of the soil seed bank, and iii) the species composition and distribution of regenerating tree seedlings present.

Differential responses to such elements and characteristics of these forest patches by such varied animal seed-dispersers as small understory birds and terrestrial monkeys have important implications with regard to regeneration patterns.

Overall Aim and Specific Objectives:

The overall aim of this research is to identify key elements of tropical forests which can be managed so as to achieve sustainable levels of forest resource use while ensuring continued functioning of the dynamic ecological processes necessary to maintain the rich biological diversity of the same forests. Toward this aim, we shall focus on four specific objectives: **A.** To study the roles of selected bird and monkey seed-dispersers in transporting seeds from closed, intact forest patches to natural and human-disturbed, secondary forest patches and forest clearings. **B.** To examine aspects of vegetation composition and structure that influence movement and feeding patterns of fruit-eating animals and consequently seed flow into these secondary patches. **C.** To assess the consequences of different dispersal patterns in terms of the rapidity and diversity of natural regeneration of tree species. **D.** To identify the key elements of this seed dispersal/regeneration system that might be necessary and/or useful to incorporate into forest management plans toward achieving the overall aim.

II. NATIONAL SCIENCE FOUNDATION PROPOSED WORK:

Title: Tropical Forest Regeneration: Influence of Animal Seed-Dispersers

Objectives of This Study:

The long term goals of this study are to develop guidelines for tropical forest management. This will require an understanding of how species interact to maintain diversity. A longer term goal is to find appropriate ways to manipulate natural processes to compensate for altered disturbance regimes and direct human exploitation. Thus far, each step in our study of the Nyungwe Forest (see Work History, 4.0) has led us to new insights from basic ecological observation to the emerging framework for management guidelines. The following series of objectives will outline the range of steps we will follow in this research effort.

Specific Objectives:

A To predict the seed shadow (seed dispersion pattern) for representative tree species based on the feeding behavior and movement patterns of their dispersers. (The seed shadows depend not

only on the type and behavior of the disperser, but also on the distribution of forest patches if dispersers modulate their movement patterns according to forest structure or constituent tree species.)

B To determine for the same representative trees how the survival of seeds to maturity in different forest patches differs. To determine the relative value of escape from adult conspecific versus dispersal to safe germination sites. Differences among the tree species will indicate the relative value and sensitivity to the dispersion pattern of their seeds.

C To use the information from B to determine which characteristics of the seed dispersion pattern favor regeneration of the set of tree species.

D To determine how seed dispersion pattern are influenced by different groups, or characteristics, of animals dispersers, for example, the size of disperser or the movement pattern of disperser (wide-ranging versus sedentary).

E To combine the answers to objectives A through D, determine the key elements/aspects of seed dispersal and seed survival that combine to predict the pattern of forest regeneration.

F To use the set of disperser-associated expectations to predict the consequences for forest regeneration patterns (i.e., changes in forest composition) due to the loss or rarefaction of particular animal dispersers. This will be tested in a secondary site (Kitabi site)

G At a site with a greatly reduced complement of dispersers of large-seeded trees, document the differences in forest regeneration patterns from seed rain to expected sapling replacement trajectories and use the results to test the predictions developed in F.

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