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Project Title:

MAINTAINING FRUGIVORE POPULATIONS: IMPLICATIONS FOR CONSERVATION OF TROPICAL FORESTS.

Principle Investigator:
Richard W. Wrangham
Peabody Museum
Harvard University
Cambridge
MA 02138

Co-Investigators
Dr. Colin Chapman
Dept. of Zoology
University of Florida
Gainesville
FL 32611
(904) 392-1196

Dr. Gilbert Isabirye-Basuta
Makerere University Biological Field Station
P.O. Box 409
Fort Portal
Uganda

Dr. John Kasenene
Makerere University Biological Field Station
P.O. Box 409
Fort Portal
Uganda

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USAID Project Officer:
Michael Benge
R&D/Comp
Room 515E, SA-18
AID
Washington, DC 20523-0218

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3) Executive Summary

Tropical forests and the animals that they maintain are being harvested at an alarming rate in many areas of the world. Since it is not always possible to protect such forests, questions concerning how the regeneration of tropical forests proceed and what factors aid in that regeneration become of prime importance. In tropical forests, the animals that eat fruit and fruit producing trees are highly dependent on each other; the frugivores require the fruit as a food source and the plants require the animals to disperse their seeds. It was these facts and perspectives that led to the establishment of the original goals of the project.

The overall objective of this project has been to investigate the role that animals play in the regeneration of forest, both in natural settings and in humanized landscapes, such as forests after logging. We first quantified the relationship between seedling recruitment of a number of tropical tree species and the behavior of frugivores and seed predators. On the basis of 1261 hours of observation, we determined which diurnal frugivores fed on fruit from these tree species and quantified each frugivore's activity. The fate of dispersed and non-dispersed seeds and seedlings was examined experimentally. Our findings suggest that a tradeoff exists between factors that promote seedling growth in areas with high seedling density and factors that promote dispersal by frugivores. From this solid scientific basis we have initiated three programs to apply the results that we obtained: (1) to identify the loss of species biodiversity that would result with the removal of seed dispersers from an ecosystem (e.g., what is happening in areas where commercial or subsistence hunting is common), (2) since it is critical that the scientific community understands the processes limiting the regeneration of tropical forests, we quantified the nature of the forest regeneration occurring in logged and unlogged areas of the Kibale National Park, and (3) to be able to initiate informed management plans of harvested or degraded areas, we examined the rehabilitation of degraded areas and the role of animals in that rehabilitation.

The first study identifies the loss in tree biodiversity that might result from subsistence and commercial hunting which have impacted large tracks of forest, but have left their physical structure relatively unaltered. The second study illustrated that logged areas of Kibale were not regenerating at the rate predicted by forestry models and quantified which regenerative processes had been altered by the logging. The third study was designed to help in understanding and predicting how forests would regenerate after specific types of degradation and suggest possible avenues that could be used in informed management plans to increase biodiversity (e.g., we are evaluating the value of pine and cypress plantations as a means of permitting indigenous trees to become established on derelict tropical land that would not be restored without human intervention).

In addition to these research programs, we have established long-term monitoring programs which will continue after the USAID project is over and will contribute useful data to the management plans of Kibale National Park. With the termination of this grant a number of collaborations, and training programs will continue. We will continue to work together (North Americans and Ugandans) on the long-term monitoring programs we have established. Through the International Studies Office, University of Florida, we have established a field training program in tropical conservation and ecology for North American and East African students. This program has already received outside University and Foundation support and thus will continue in the foreseeable future. We trained a number of students (both Ugandan and North American), and many of these students will continue to work in Uganda. This grant facilitated the establishment of a good working relationship with the Park Warden of Kibale National Park, and it is envisioned that we will provide information useful in the formulation of the parks management plans, which will be drafted next year.

4) Research Objectives & 5) Methods and Results

Two conspicuous features of tropical forests are the production of fleshy fruits by the majority of the plant species and the large numbers of animals that eat fruit (Frankie et al. 1974, Howe 1989). Frugivores and plants are highly dependent on each other; the frugivores require the fruit as a food source and the plants require the animals to disperse their seeds. Despite the numerical abundance of such species little is known about the interdependence of the species involved. Thus, the objective of this research has been to understand the complex interactions that exist between fruiting trees and the animals that ingest and disperse their seeds. We initially established detailed observations of frugivore activities, documented fruit removal, and set up long-term monitoring of the fate of dispersed and non-dispersed seeds and seedlings. Once, we were in the long-term monitoring stage of this work we initiated three programs to apply the results that we were obtaining: (1) to identify the loss of species biodiversity that would result with the removal of seed dispersers from an ecosystem (e.g., what is happening in areas where commercial or subsistence hunting is common), (2) since it is critical that the scientific community understands the processes limiting the regeneration of tropical forests, we quantified the nature of the forest regeneration occurring in logged and unlogged areas of the Kibale National Park, and (3) to be able to initiate informed management plans of harvested or degraded areas, we examined the rehabilitation of degraded areas and the role of animals in that rehabilitation.

We have continued our long-term monitoring of frugivores and the fate of dispersed seeds. The results suggest that selection may alternatively favor small seed size, with an increased probability of dispersal when frugivores are common, and large seeds with enhanced seedling vigor when frugivores are rare and seeds are not dispersed (Chapman and Chapman 1995, Chapman and Chapman submitted). We now have almost 3 years of data in the Kibale Forest National Park, Uganda which examines the relationship between the ability of six tree species to recruit under vs away from parent trees, and the behavior of frugivores and seed predators. Based on 1261 hours of observations, we determined which diurnal frugivores fed on fruit from these tree species and quantified the magnitude of each frugivore's activity. Subsequently, we experimentally examined the fate of dispersed and non-dispersed seeds and seedlings. A total of 3170 seeds and 260 seedlings were placed at stations away from parent trees and 456 seeds and 115 seedlings (of four of the species) were placed under adult conspecifics. To date, evidence suggests that for Mimusops there is a clear advantage to dispersal at both the seed and seedling stages; seeds placed away from adult conspecifics have a 8% lower probability of disappearing than seeds under adults and seedlings away from adults have a 30.3% greater probability of surviving than seedlings under adults. For Pseudospondias, all seeds whether placed under an adult or away from an adult disappeared, but seedlings growing away from adults have a 24.2% increased probability of surviving when compared to seedlings growing under conspecific adults. For Uvariopsis, dispersed seeds had a 56% greater probability of disappearing than seeds directly under a parent tree, while at the seedling stage there was little difference in the probability of surviving. For Balanites, 5% of the seeds placed under an adult conspecific disappeared, while none of the seeds planted away from adults disappeared, and seedling mortality under the parent averaged 3%, while mortality away averaged 6.4%. The percentage of the fruit crop removed from focal trees was correlated with non-dispersed seed and seedling disappearance, suggesting that the ability to survive

under an adult may alter other aspects of the tree's life history. Our findings support the idea that a tradeoff exists between factors which promote seedling growth in areas with high seedling density and factors which promote dispersal by frugivores, and that selection has favored different species to adopt different strategies, depending on the behavior of dispersers.

In addition to this major focus we have initiated three applied programs: (1) to identified the loss of species biodiversity that would result with the removal of seed dispersers from an ecosystem, (2) to understand the processes limiting the regeneration of tropical forests, we quantified the nature of the forest regeneration occurring in logged and unlogged areas, and (3) to be able to initiate informed management plans of harvested or degraded areas, we examined the rehabilitation of degraded areas and the role of animals in that rehabilitation.

1) Survival without Dispersal?

The loss of tropical forest is a central conservation issue, and much effort has been invested into understanding the extent of forest conversion, the factors contributing to its loss, and possible solutions to decrease the rate of destruction. However, human activities in forests are not limited to the cutting of trees. Subsistence and commercial hunting have impacted large tracks of forest, but have left their physical structure relatively unaltered (Redford 1992). Unfortunately, there is little understanding of how these hunting activities alter the processes governing the maintenance and long-term sustainability of forest ecosystems (Terborgh 1988; Wrangham et al. 1994). For example, large animals are the most preferred species for hunters, and it may be that these species play particularly significant roles in the dispersal of large seeded tropical trees. For example in Kibale, we have demonstrated that although chimpanzees constitute only 1.4% of the primate frugivore populations by numbers and 14.2% of the primate frugivore biomass, they are responsible for an estimated 45.3% of the seeds defecated by the frugivorous primates (Wrangham et al. 1994).

Such findings support the idea that seed dispersal by frugivores is vital to the survival of fruiting tree populations, since the survival of fallen fruit does not appear to be sufficient to maintain populations of many tropical tree species. A number of species specific studies examining seedling survival under parent trees have found little or no recruitment under parent trees (Howe et al. 1985). However, other studies reveal relatively small differences in the probability of survival between seeds under parent trees and those dispersed away (DeSteven & Putz 1984). Such conflicting results make it difficult to predict the consequences of a reduction in frugivore populations on plant biodiversity.

Based on a sample of 25 tropical fruiting tree species we identified the proportion of tree species that have many conspecifics growing under parent trees and the proportion of species that do not. The objective of this analysis was to provide an initial assessment of the extent of loss of biodiversity that "might" result from a significant reduction in populations of seed dispersers.

If one considers only those species that had no seedlings under parent trees, but many seedlings away from the parent, then removal of frugivore seed dispersers would result in a 4% decrease in species richness of fruiting trees in a single generation. It is likely that tree species that had no (or very few) conspecific seedlings under the adults (none large) and few seedlings away are also unable to recruit individuals into the adult population with the absence of seed dispersers. If we combine these categories, then 60% of the trees would be lost if frugivores were removed.

In reality, hunting is likely to cause the removal of only a few seed dispersing species, while the majority of frugivore populations will be reduced in size. However, the most susceptible species to hunting will be the larger bodied frugivores. It is interesting that Mimusops bagshawei, a species that shows no evidence of recruitment under the parent tree, is very reliant on chimpanzees for much of its seed dispersal. From focal tree observations, and counts of the fruits eaten by all diurnal frugivores attending M. bagshawei trees, we have estimated that 34.5% of the fruits processed at M. bagshawei trees are eaten by chimpanzees. Such species that are highly dependent on large-bodied frugivores, may be particularly susceptible to extinction under increased hunting pressures.

2) Regeneration of tropical forests after logging: examination 30 years post-harvest.

It is critical that the scientific community understands the processes limiting the regeneration of tropical forests after different types of anthropogenic disturbance. Tropical forests are being converted to agricultural land or destructively logged at an ever increasing rate (Whitmore and Sayer 1992, FAO 1993). As a result, there will be an increased tendency to relog previously harvested areas or, following political or economic change, to restore degraded areas to productive lands. In both situations we must be able to both predict the direction and time scale over which regeneration will occur, and understand the processes that will influence the time scale.

Early estimates of cutting cycles were based simply on typical growth rates of tropical forest trees and average levels of felling damage (Dawkins 1959). These estimates ignored other processes that may alter rates of regeneration. Inventory data and estimates of the growth and mortality rates of cohorts of trees have recently been used to provide a basis for harvesting schedules (e.g., Usher 1966, Vanclay 1989). However, such models suffer from ignoring differential growth rates between species, using the mean growth rate which may be inappropriate, and unreliable mortality estimates due to episodic and spatially clumped mortality events. Further, such stand models should be restricted to areas with conditions similar to the sites on which the model's parameters were based (Putz 1993). This limits the general applicability of such models because they do not incorporate a number of parameters that often vary between areas and could influence regeneration rates. Important parameters include soil fertility (Ewel, 1980), the nature of skid damage, soil compaction, and erosion following logging and bulldozer activity (Douglas et al., 1992; Cannon et al., 1994; Uhl et al., 1982), extensive herb or shrub layer growth (Fitzgerald & Selden, 1975; Brokaw, 1983; Kasenene, 1987), and the probability of fire inhibiting regeneration in the flammable degraded land (Woods, 1989; Nepstad et al., 1991; Uhl & Buschbacher, 1985; Uhl et al., 1981; 1988a,b,c; Uhl & Kauffman, 1990; Janzen,

1988). In addition, the extraction level (stems/ha), extent of damage (% of trees lost), and nature and degree of canopy opening are highly variable between different extraction schemes. Selective logging typically results in the damage of 50% of the trees in the area, but can vary from 6% of the trees (White 1994, Wilkie et al. 1992) to 57% (Johns 1988). The extent of variability in key parameters makes it difficult to construct predictive models that will be broadly applicable and provide accurate estimates of reasonable logging schedules. The development of more effective models depends on a better understanding how different logging intensities and protocols affects the processes underlying seedling establishment, tree recruitment, growth, fruiting phenology, and tree mortality.

We quantified the nature of the forest regeneration occurring in different areas of the Kibale National Park, some areas were unlogged, while other areas were logged nearly 25 years ago at different intensities. We predicted that recruitment and growth processes would be accelerated in logged areas relative to unlogged areas, facilitating increased recruitment of trees into the adult size classes following logging. To do this study, we quantified the growth and mortality rates of trees $\geq$ 10 cm DBH (diameter at breast height Chapman et al. 1994) and stand structure of all trees in areas that had experienced different levels of logging pressure or no logging (from 0.1 cm DBH up). We also quantified the forest phenology, seed rain, seed bank, and seedling density in logged and unlogged areas.

The unlogged areas experienced the lowest tree mortality rate of any of the sites; the most heavily logged site had the highest mortality rate (a 74.1% increase relative to one unlogged site). Compared to the logged areas, the unlogged compartments had more trees die standing, and fewer apparently health trees die as a result of being knocked down by adjacent tree falls.

Trees in the most heavily logged areas had the slowest growth rate of any of the areas. There was no difference in seedling density in logged and unlogged forests, nor in the number of species of seedlings found in the quadrats. Similarly, the number of seedlings that could have come from trees directly above the sampling site did not vary between logged and unlogged areas. Interestingly, there was a tendency for seedlings from "desirable" timber trees (as classified by Kingston 1967) to be more common in the logged areas examined, than in the unlogged forests.

Fifteen species of seeds were found in soil samples from the logged and unlogged forests examined. Seven species of seeds were found only unlogged forest, 4 species were only found in the logged area, and 4 species were found in both areas. On average, the number of species found at a sampling site was higher in unlogged area, than in the unlogged area. In contrast, there was a tendency for the number of seeds found in the seedbank in the logged area to be higher than in unlogged area (see also Guevara & Gomez-Pompa 1972, Hopkins and Graham 1984). However, for both areas these averages were highly skewed by a few sites with a large number of seeds from one species.

Indices of fruit production (Chapman et al. 1994) indicated that more fruit was produced in unlogged than in logged areas. In terms of maintaining frugivore abundance, particularly species with small home ranges, the number of months with very low fruit production may be particularly important. In the unlogged areas, only 10% of the months had fruit abundance scores (fruiting trees/ha * score) $\leq$ 50. Low fruit scores occurred much more frequently in logged areas. Fruiting scores were $\leq$ 50 for 34 months at in one logged area and 17 months at another logged area.

Several processes of forest dynamics differ between the areas that had been logged approximately 25 years ago and the unlogged areas in Kibale Forest. One would envision that 25 years should be sufficient time to permit an initial quantification of the forest's regenerative responses to the conditions created by different logging regimes. Post-logging mortality, growth rates, and stand structures differed between areas. Mortality was highest in the heavily logged areas and many deaths result when healthy trees were knocked over by adjacent tree falls (Kasenene 1987). Tree growth rates in the most heavily logged area were consistently slower for all size classes. In contrast, the most lightly logged area had similar growth rates to the unlogged areas in the small size classes, but trees in the 30 to 50 cm DBH size cohort exhibited elevated growth rates relative to the unlogged area. This pattern was supported through examination of stand curves in the different compartments. The stand curves suggest that in the smallest size classes the most lightly logged area had a slightly greater density of trees than unlogged area, but otherwise they are similar up to the largest sizes classes. In contrast, the density of all size classes of trees was consistently lower in both of the heavily logged areas when compared to the unlogged area. Consequently, many of the gaps created by harvesting in these heavily logged areas still exist and have not been filled in by new tree growth.

A number of studies have shown that when mature tropical forest is cut and light levels at ground level are increased, colonizing woody and herbaceous species quickly invade (e.g., Hall and Swaine 1980, Hopkins and Graham 1984, Vazques-Yanes 1976, Howe et al. 1985, Hopkins et al. 1990). The documented differences in mortality, and growth rates between logged and unlogged areas in Kibale may relate to light conditions created following logging. To manage a natural forest effectively, light levels required for optimal growth must be known. Although it is generally thought that canopy species survive and grow better in sun than in shade (Brokaw, 1985; Putz 1993), this is not always the case. Some species in Kibale exhibit decreased survivorship and slower growth rates in gaps than under closed canopy. In a low diversity forest like Kibale, there may be few tree species that can take advantage of openings created by high intensity logging. This process may account for the fact that many of the large canopy openings are presently dominated by an aggressive herbs and shrubs (primarily Acanthus pubescens). Kasenene (1984, 1987) documented that, approximately 10 to 15 years post-harvest, areas that were logged had more ground vegetation cover than unlogged areas, and that there was a negative correlation between seedling and sapling richness and the density of ground vegetation. Once a dense herb or shrub layer is established, it may inhibit seedling survival. We found no difference in the density or species richness of seedlings in the logged and

unlogged forests. Further, the number of seedlings that emerged from the disturbed soil (seedbank + seedrain) and initially seed-free soil (seed rain) was greater in the logged forest than the in the unlogged forest. However, sapling density was much lower in the heavily logged areas. Therefore, we are seeing much lower recruitment into the sapling class in logged areas, which may relate to the dense shrub layer.

3) Rehabilitation of Degraded Lands in Africa

Tropical forests and the animals they support are being increasingly threatened by accelerating rates of forest conversion and degradation. In an ever changing political world, it is often unfeasible to protect areas from such conversion until the political and economic systems change. Once the political environment is suitable to pursue conservation or management goals, the forests have often been converted to other uses. The need to increase the value (intrinsic or economic) of degraded forests has lead to a growing area of ecological research. However, there is often little quantitative data available to tropical forest managers regarding the potential success of various management options.

Typically forest succession in the lowland tropics is extremely rapid, however in a number of situations succession can be extremely slow, or it may not proceed at all. For instance, the area may be characterized as too dry or as having soil of too poor fertility (Ewel, 1980), there may be extensive skid damage and erosion following logging or bulldozer activity (Douglas et al., 1992; Cannon et al., 1994; Uhl et al., 1982), reforestation may be inhibited by extensive herb layer growth (Fitzgerald & Selden, 1975; Brokaw, 1983; Kasenene, 1987), or since the degraded land is generally far more flammable than the forests that were replaced(Woods, 1989; Nepstad et al., 1991; Uhl & Buschbacher, 1985; Uhl et al., 1981; 1988a,b,c; Uhl & Kauffman, 1990; Janzen, 1988), fires set by neighboring agriculturalists may be difficult to control and may inhibit regeneration.

It has been suggested that tree plantations should be considered as a means to restore the productivity of the land and potentially as a means of restoring some of the original biodiversity (Lugo 1992). However, for plantations to be a component of a management strategy that has the goal of rehabilitating a community similar to that prior to conversion, it must be demonstrated that indigenous tree species can become established under plantations and that the logging of the plantation will not destroy the indigenous trees that had become established.

We evaluated the value of pine (Pinus caribaea, Pinus patula) and cypress (Cupressus lusitanica) plantations as a means of permitting indigenous trees to become established on derelict land in the Kibale. In Kibale forest regeneration following clearly for agricultural purposes or following selective logging is suppressed by an aggressive growth of the herb layer, thus unmanaged land tends to remain derelict land of little value, either intrinsic or economic.

We found that there were 47 species of indigenous trees in eighty 10 m by 10 m quadrants. The mid-altitude forest of Kibale is a relatively species poor area, thus this is a relatively large proportion of species found in the area. Data from a

long-term phenological study provides a perspective. 78 species of trees have been identified from in a system of 26 transects (200 m by 10 m = 5.4 ha). There were between 5 and 38 indigenous tree species greater than 2 m tall found in a single quadrant. As with species richness, the number of trees varied between treatments (unlogged P. patula mean = 18.5, unlogged P. caribaea mean = 20.1, logged P. patula mean = 17.5, logged C. lusitanica mean = 13.3). Tests indicate that areas of unlogged P. caribaea had significantly more trees than areas where C. lusitanica had been logged. In all cases damage caused by the logging or by changes in the ecological conditions following logging, resulted in a reduction in the number of trees in the quadrant, however the magnitude of the reduction was small and was not significant in the only paired comparison (logged mean = 17.5 trees vs unlogged 18.5 trees P. patula).

6) Impact, Relevance, and Technology Transfer

The study had the explicit objective of first developing a firm scientific understanding of how specific principles of seed dispersal and seedling mortality influences the regeneration process. Subsequent developing on these studies, we attempted to apply the results in ways that were useful to Uganda in general and specifically to the Kibale National Park. We conducted a number of specific studies that had direct application to the management of forests in Uganda or elsewhere in the tropics. Specifically, we investigated how regeneration of natural trees would progress under pine plantations. This information would help managers determine if it was feasible to encourage regeneration of indigenous forests through the planting of conifer plantations. The logic is that the conifer plantations would be financially feasible, since there will be a dollar return at the time of harvesting. The project would only be viable (e.g. Kibale National Park) if the indigenous trees were able to regenerate under the conifers. The reason to expect indigenous trees to be unable to do so, is that it seemed unlikely that many of the tree species that rely on animal dispersal, would be able to disperse seeds into the conifer plantations, since we did not envision that animals would enter the conifers. Surprisingly, the results show that animals do enter the conifers, that many species of animal-dependent tree species have seeds dispersed into the plantations, and that the regeneration of the indigenous trees is substantial.

The second applied study involved assessing the processes of regeneration in logged and unlogged forests. This project was developed to investigate if the logged forest was regenerating at a rate predicted by forestry models, and if it was shown not to follow the model's prediction to understand why. Here we were able to show that in forests like Kibale, where there are few aggressive colonizing tree species, tree regeneration following logging is slowed by the invasion of aggressive herb layers. This suggests that regeneration will be slowed and suggests that in Uganda alternative logging models should be employed. Alternatively, it suggests a number of inexpensive management practices that could be used to accelerate regeneration. At the present time two students are developing this theoretical line of work, and are testing the applicability of one simple management scheme.

The third applied study examined the probable long-term consequences of the removal of seed dispersers from the forest - a likely consequence of commercial or subsistence hunting. This provides information useful to the Park Warden to encourage the effective endorsement of game regulations.

It is envisioned that this information will be of value to Parks, when they make the management plan of Kibale, and to the Forest Department, when the plan management schemes for other areas (Kibale is no longer under the control of the Forest Department). Both groups have been provided a full description of the results of these studies.

The USAID grant has facilitated training, both at Makerere University in Uganda and students from the U.S. (see below for detailed description and listing of the students that have received training). This has built the institutional capabilities of Makerere University and the Forest Department (where one Uganda student that worked on forest regeneration in Kibale is currently employed). This training has the potential to have great future ramifications since individuals are

now in place with the training, skills, and ideas necessary to further this area of research and development.

The re-gazetting the Kibale from a Forest Reserve to a National Park, has been a great achievement, however it has resulted in a change in government personnel that we have been dealing with. This has been profitable, in that the results and concepts presented in our program have now reached two different government departments, however it has taken additional time and effort.

We initiated the first long-term field course in "Tropical Ecology and Conservation" which was held at Makerere University Biological Field Station. The teaching of field courses is part of the long-term sustainability plan designed for the field station, and the University of Florida is attempting to contribute to that plan. The course instructors were Drs. Colin Chapman, Lauren Chapman, G. Isabirye-Basuta, John Kasenene, and Tom Crisman. There are already plans for the course to be taught again next year. The course has received funding from the Florida University system and from foundations, thus it will continue for the foreseeable future. The orientation of the course is that students from the United States and students from East Africa participate jointly in the courses, exchanging ideas and experiences. During the three years the course has been taught it has been a great success and hopefully, the success will continue in future years. This course has the potential to get information, such as that concerning the role of animals in the regeneration of natural forest, into the hands and minds of many individuals.

7) Project Activities/Outputs

List of Publications

The following are publications resulting directly or indirectly from the award:

a) Studies anticipated in the proposal

Frugivory and the Fate of Dispersed and Non-Dispersed Seeds In Six African Tree Species.
C.A. Chapman and L.J. Chapman.
Journal of Tropical Ecology (Submitted).

Exotic Tree Plantations and the Regeneration of Natural Forests in Kibale National Park, Uganda
C.A. Chapman and L.J. Chapman
Biological Conservation (Accepted with Revisions).

Conservation and Sustainable Development in the Lake Victoria Basin:
Ecological First Aid to Buy Time.
L.J. Chapman, C.A. Chapman and L. Kaufman.
P. Schmidt, A. Goldman, T. Crisman, R. Cohen (eds.). University of Florida Press, Gainesville (Accepted with Revisions).

Tropical Forests of East Africa: A History of Disturbance and Regeneration.
C.A. Chapman and L.J. Chapman.
Ecosystems and Their Conservation in East Africa.
T.R. McClanahan and T.P. Young (eds.). Longman, London. (In Press).

Social Ecology of Kanyawara Chimpanzees: Implications for the THV Hypothesis.
R.W. Wrangham, C.A. Chapman, A.P. Clark-Arcadi and G. Isabirye-Basuta.
The Great Apes Revisited. W.C. McGrew, L.F. Marchant, and T. Nishida (eds.).
Cambridge University Press, Cambridge. (In Press).

Survival Without Dispersers?: Seedling Recruitment Under Parents.
C. A. Chapman and L. J. Chapman. 1995.
Conservation Biology 9:675-678.

Indices of Habitat-Wide Fruit Abundance in Tropical Forests.
C.A. Chapman, R. Wrangham, and L.J. Chapman. 1994.
Biotropica 26:160-171.

Seed Dispersal By Forest Chimpanzees.
R. Wrangham, C.A. Chapman, and L.J. Chapman. 1994.
Journal of Tropical Ecology 10:355-368.

Frugivores and Fruit Syndromes: Differences in Patterns at the Genus and Species Levels.
K. Fischer and C.A. Chapman. 1993.
Oikos 66:472-482.

Thesis Produced:

W. Olupot. Masters in Biology, Makerere University.
Thesis Title: Range Use in Mangabeys: Influence of Interspecific Communication Concerning Discovery of Food Sources.

b) Studies not anticipated in the proposal.

Mangebey (*Cercocebus albigena*) Ranging Patterns in Relation to Fruit Availability and the Risk of Parasite Infection in Kibale National Park Uganda.
W. Olupot, C.A. Chapman and G. Isabirye-Basuta.
African Journal of Ecology (Submitted).

Wetland Ecotones as Refugia for Endangered Fishes.
L.J. Chapman, C.A. Chapman, and M. Chandler.
Biological Conservation (Accepted with Revisions).

Primate Seed Dispersal: Coevolution and Conservation Implications
C.A. Chapman
Evolutionary Anthropology (In Press).

Predation on Primates: Where Are We and What Next?
S. Boinski and C.A. Chapman
Evolutionary Anthropology (In Press).
Hypoxia Tolerance in Twelve Species of East African Cichlids: Potential for Low Oxygen Refugia in Lake Victoria.
L.J. Chapman, L. Kaufman, C.A. Chapman, and E. McKenzie.
Conservation Biology (In Press).
Refugia for the Endangered Fish Fauna of Lake Nabugabo, Uganda.
L.J. Chapman, C.A. Chapman, R. Ogutu-Ohwayo, M. Chandler, L. Kaufman, & A. Keiter.
Conservation Biology (In Press).
Biodiversity, Conservation, and the Great Lakes of East Africa.
L. Kaufman, C.A. Chapman and L. J. Chapman.
Ecosystems and Their Conservation in East Africa.
T.R. McClanahan and T.P. Young (eds.). Longman, London. (In Press).
Mixed Species Primate Groups in the Kibale Forest: Ecological Constraints on Association.
C.A. Chapman and L.J. Chapman. 1996.
International Journal of Primatology 17(1).
Habitat, Annual, and Seasonal Effects on Positional Behavior in Red Colobus Monkeys.
D.L. Gebo and C.A. Chapman. 1995.
American Journal of Physical Anthropology 96:73-82.
Positional Behaviour in Five Species of Old World Monkeys.
D.L. Gebo and C.A. Chapman. 1995
American Journal of Physical Anthropology 97:49-76.
Ecological Constraints on Group Size: An Analysis of Spider Monkey and Chimpanzee Subgroups.
C.A. Chapman, R. Wrangham, and L.J. Chapman. 1995.
Behavioural Ecology and Sociobiology 36:59-70.
Contrasting Chimpanzees and Pygmy Chimpanzees: Nearest Neighbor Distances and Choices.
F. White and C.A. Chapman. 1994
Folia Primatologica 63:181-191.
Mangabey (*Cercocebus albigena*) Population Density, Group Size, and Ranging: A Twenty-Year Comparison.
W. Olupot, C.A. Chapman, C. Brown and P. Waser. 1994.
American Journal of Primatology 32:197-205.
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Folia Primatologia 61:31-34.
Measuring Chimpanzee Food Abundance.
R.K. Malenky, R. Wrangham, C.A. Chapman and E.O. Vineberg. 1993.
Tropics 2:231-244.

List of Students Trained and Topic of Research

Students completed:
W. Olupot. Masters in Biology, Makerere University.
Thesis Title: Range Use in Mangabeys: Influence of Interspecific Communication Concerning Discovery of Food Sources.

Students in Progress:

Ph.D.

Lisa Naughton University of Florida
Crop raiding, wildlife, and subsistence farmers near Kibale National Park, Uganda.
Sophia Balcomb
The responses of primates to the spatial and temporal variation in ecological conditions.
William Olupot Purdue University
Topic undecided.

Masters

Scot Duncan University of Florida
Seed dispersal by bats of seeds into regenerating areas.
Ginger Shepherd University of Florida
Secondary seed dispersal by dung beetles.
Daphne Onderdonk University of Florida
The survival of primates in forest patches.
Amy Kaplan University of Florida
Seed dispersal and the ultimate distribution patterns of tropical forest trees.
Laura Sirot University of Florida
Factors affecting the density of primates in logged forest: a reevaluation after 30 years post-harvest and 15 years post census.

List of Meetings Attended

The Role of Wetlands in the Maintenance of Fish Faunal Structure and Diversity in the Lake Victoria Basin - With L.J. Chapman and T.L. Crisman.
XXVI Int.l Congress of Theoretical and Applied Limnology - July, Sau Paulo, Brasil

Survival Without Dispersal: The Fate of Non-Dispersed Seeds?
Florida Ecological and Evolutionary Symposium. - April 1994

Frugivory and the Fate of Dispersed Seeds in Kibale Forest, Uganda.
Invited Lecture - Dept. of Zoology. University of Florida. February 1993.

Forest Primate Conservation: Concepts and Problems.
Invited Lecture - Purdue University, February 1993.

Frugivory and the Fate of Dispersed Seeds in Kibale Forest, Uganda.
Invited Lecture - Purdue University, February 1993.

Forest Primate Conservation: Concepts and Problems.
Invited Lecture - Northern Illinois University, February 1993.

Twenty Years of Primate Population Densities.
With P. Waser, W. Olupot, and C. Brown.
Ecological Society Meetings, July 1992.

Developing Standard Methods For Assessing The Availability of Fruit and Herbaceous Food in African Ape's Habitat - with R.K. Malenky.
International Primatology Meetings, Strasbourg, France, August 1992.

Positional Behaviour and Habitat Use in Cercopithecoid Monkeys. - with D.L. Gebo.
American Association of Physical Anthropologists, April 1992.

3) Project Productivity

From an academic perspective the project was able to meet the goal set out in the proposal: to investigate the role that animals play in the regeneration of forest, both in natural settings and in humanized landscapes, such as forests after logging. These results are reflected in the publications that have been produced, and those that will be produced in the future. However, we have been able to accomplish a number of goals, not specifically mentioned, or only mentioned in an abstract fashion in the proposal (e.g., specific students have received training and degrees).

In general, there were no major deviations from the original plan. With the exception of some planned activities involving the team of researchers in Nyungwe, Rwanda. Because of the war in Rwanda, it was not possible to complete all planned activities envisioned. We have been attempting to combine the results obtained here with those obtained from the USAID funded Nyungwe Project in Rwanda. Both projects had similar orientations, and comparisons between the two will greatly increase the generality of the results that can be reached. As a result of the political problems in Rwanda, that project has closed down, however we were still able to continue and extend the collaboration. Dr. T. Moermond, the Nyungwe Project leader, Dr. R. Fimbel and Dr. C. Fimbel the (USAID local representative and WCS representative respectively for Nyungwe) have come to Kibale to exchange ideas and to initiated joint projects in Kibale (the project on regeneration under pines was done in conjunction with the Dr. R. Fimbel and Dr. C. Fimbel). Students (Erica Paige Cochrane) that were working at the Rwanda site have changed their research plans and now will work in Kibale; extending the future collaboration and greatly enhancing the transfer of knowledge between the projects.

Training of Ugandan and North American students has been a primary goal of the project. William Olupot, a Ugandan student completed his research, submitted his Masters thesis, and we have now arranged for him to attend Purdue University here in the United States to work towards a Ph.D. degree (with field work conducted at Kibale). Jerry Lwanga, has completed his Ph.D. thesis at the University of Florida and has returned to Uganda and is presently working with the Forestry Department. We have also arranged World Bank funding for John Olowo to come from Uganda to the University of Florida in August 1995 to start working towards his Ph.D.. Seven graduate students from the University of Florida (who were funded independent of this grant, but benefitted by the logistical support made possible through USAID) are presently working on aspects of the research programs that we have not addressed previously.

This PSTC project involves Drs. Gilbert Isabirye-Basuta (co-Director of the Makerere University Biological Field Station) and Dr. John Kasenene (Research Scientist). This last year these Ugandan collaborators, Dr. Lauren Chapman, and the new Park Warden drew up the research priorities for the field station. Also, we have participated in programs to build the library at the field station, prepare advertisements for the field station, and assist in the general planning of the required infrastructure for researchers and field courses.

With the resettlement of encroachers from the southern third of Kibale, the National Park has been very interested in restoration, thus we have been working with them on various aspects of forest regeneration in abandoned agricultural areas and have been addressing questions such as how crop raiding by animals in the park will affect neighboring agricultural land (Lisa Naughton from the University of Florida is just completing her Ph.D. thesis on the topic, based on research done in Kibale).

9) Future Work

We have a long-term commitment to the Kibale Forest and the scientific and applied research that is conducted there. As a result a number of the programs will continue in the future. With funding from National Geographic, we are continuing the long-term monitoring of tree phenology and mortality. With assistance from the Florida State Universities and foundation support we will continue to offer the course in tropical conservation and ecology taught each summer at Kibale Forest. We envision that we will contribute information that will be useful in the formulation of an informed management plan for Kibale Forest, providing the information requested by the new Park Warden. In addition, there are a number of potential scientific endeavors that we are currently initiating and seeking funding to enlarge. Currently, in Kibale, there is an excellent opportunity to combine an academic study of restoration ecology, with the goal of obtaining information vitally needed for the construction of an informed conservation and management plan. The southern third of Kibale experienced agricultural encroachment for over a decade. However, on April 1st 1992, the government successfully resettled 30,000 people and is now attempting to restore the biological integrity of the area and in November 1993 the area was declared a National Park.

Little is known about the process of regeneration in different tropical areas of the world (particularly in Africa), and the effectiveness and consequences of different forms of human intervention are poorly understood. However, work in Latin America suggests a basic cycle of events in which three factors potentially limiting regeneration: (1) lack of seeds reaching disturbed sites, (2) predation of seeds that do arrive, and (3) seedling mortality. In each of these three steps animals play vital roles in the regeneration process.

Based on our past work, we propose to initiate a study the role of fruit and seed eating animals in the restoration of abandoned croplands in the southern corridor of Kibale; information on this is vitally needed in the construction of an informed management plan for the park.

Through a survey of the natural regeneration that is presently occurring in different areas of Kibale, a detailed study of restoration in one area, and the investigation of two different management plans, we will address a series of questions:

1) How does frugivore abundance influence forest regeneration?

2) How do levels of seed predation and rodent density influence forest regeneration?

3) How does the level of degradation of the source forest influence regeneration?

4) What are the effects of distance from the forest on the number and kinds of seeds dispersed?

5) How applicable are South American studies of restoration of abandoned pastures to restoration of abandoned cropland in Africa?

6) What is the success and form of regeneration resulting from two economically and logistically feasible management plans (the sowing of seeds onto abandoned agricultural land, and the planting of cuttings that will act as focal points to attract birds and other seed dispersers to the middle of fields)?

10) Literature Cited

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