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Long-term studies reveal the conservation potential for integrating habitat restoration and animal nutrition

INTRODUCTION

Human modification of ecosystems is threatening biodiversity on a global scale. The net change in global forest area between 2000 and 2005 was $\approx$ 7.3 million ha per year ($\approx$200 km^2 of forest per day)(FAO, 2005). This does not consider the vast areas being logged selectively or the forests degraded by fire, both of which can impact huge areas. For example, during the 1997/1998 El Niño, 7 million ha of forest burned in Brazil and Indonesia alone (Chapman & Peres, 2001). And, even when the physical structure of the forest remains intact, subsistence and commercial hunting can have a profound impact on forest animal populations. For example, Chapman and Peres (2001) estimate that 3.8 million primates are consumed annually in the Brazilian Amazon.

In Uganda, the country where this study focuses, threats to biodiversity are similarly grave. Closed-canopy tropical forest once covered 20% of the country's land area, but deforestation has reduced this to just 3% (Howard *et al.*, 2000). Furthermore, Uganda lost 18% of its remaining forest between 1990 and 2000 (Howard *et al.*, 2000). The most recent estimate suggests that the annual rate of loss of tropical high forest is 7%, while that of woodland is 5% and bushland is 4% (Pomeroy and Tushabe, 2004).

One conservation strategy for addressing these pressures on tropical ecosystems is to protect specific areas in as pristine condition as possible; namely in parks and reserves. However, these Protected Areas are often small in area; and it is widely acknowledged that not all biodiversity will be maintained in such isolated, small habitats. Thus, associated with this strategy, it is anticipated that, once economic and social situations in developing countries have changed, these areas will serves as the seeds of recovery, particularly for organisms requiring resources beyond the confines of the park boundary. For this strategy to be viable requires a number of conditions to be met. First, the integrity of Protected Areas must be maintained over the time frame needed for economic and social change to occur. This is certainly a difficult task and the duration over which this change will occur is often not known. Second, the areas outside of Protected Areas must not be degraded to such an extent that recovery is arrested or does not occur on a time frame that is suitable for management. A recent review of the accumulation of vegetative biomass on degraded tropical lands suggests that the land-use practices typically used in the tropics result in lands with sufficient resources to promote regeneration in a time frame that is suitable for management (Naughton-Treves and Chapman, 2002). Unfortunately, the few available studies from Uganda suggest that rates of tree regeneration here are amongst the slowest in the world, with regeneration often being suppressed by grasses and herbs (*Acanthus pubescens*)(Naughton-Treves and Chapman, 2002; Paul *et al*., 2004). Third, and possibly most critically, the scientific community must have a working knowledge of how to restore specific plant and animal communities. This requires both long-term studies that monitor population changes over biologically meaningful timeframes and the knowledge of how to integrate information on habitat restoration and determinants of animal abundance. Unfortunately, restoration ecology historically has been biased to investigations of processes affecting plant communities. To verify this, we reviewed all the research articles published in the journal *Restoration Ecology* from 2000 to the last issue of 2006 ($n = 372$ articles; excluding invited issues). Of those articles published in *Restoration Ecology* only 11.8% involved animals or an animal-mediated process (e.g., seed dispersal, pollination). Only 1.6% of the articles published in this journal involved descriptions of the recovery or restoration of animal populations (there was a special issue on this topic in 2001 with six articles).

Given the paucity of studies that deal with restoration of animal populations, the lack of studies integrating determinants of animal abundance and restoration ecology, and the documented slow regeneration in Uganda, we initiated a series of studies in Kibale National Park, Uganda to determine the critical factors that influence the abundance of endangered red colobus monkeys (*Procolobus rufomitratus*) and sought to understand how to facilitate forest regeneration in such a way as to promote a forest that would support high red colobus abundance.

DETERMINANTS OF RED COLOBUS ABUNDANCE

As we came to know Kibale, we became intrigued by the apparent variation in primate abundance, and realized that this variation offered a unique opportunity to investigate the ecological determinants of monkey abundance. To determine the extent of variation in red colobus density, we conducted intensive line transect surveys at six sites typically every second week for 2 years (Chapman and Chapman, 1999). To establish which food resources were important, we collected more than 1000 hours of feeding observations and determined the abundance of the major food resources at each of the six sites to evaluate whether red colobus abundance was related to food availability. We found that red colobus numbers were fairly high at most sites, even in disturbed areas. However, a surprisingly low population density was found at Dura River, a relatively undisturbed riverine site in the middle of the park. As we predicted, red colobus density was related significantly to the cumulative size of important food trees, but only when the Dura River site was excluded.

We initially thought the red colobus monkeys were below carrying capacity at Dura River. A small number of censuses conducted in 1970 and 1971 (Struhsaker, 1975, 1997) estimated red colobus group density to be 2.7 times greater than what we recorded in 1996–1997. An epidemic reportedly had killed a number of male red colobus monkeys in another area of Kibale in the early 1980s (T. T. Struhsaker pers. comm.). If such epidemics are common, or if hunting by chimpanzees (*Pan troglodytes*) at this site had recently been intense, the colobus population could be below carrying capacity. However, another option to consider is the possibility of variation in food quality that may not be represented in our estimates of food availability.

Unlike most primates, colobus monkeys have a specialized alkaline fore-stomach designed for digesting high-fiber leaf material. Milton (1979) proposed that the ratio of protein to fiber in food items was a good predictor of food quality, because it reflects both nutritional value and digestibility. By using the ratio of protein to fiber as an index of mature leaf quality, several subsequent studies found positive correlations between colobine biomass and food quality at local (Ganzhorn, 2002) and regional (Oates *et al*., 1990) scales. To apply this model, we quantified the degree to which the average protein to fiber ratio of mature leaves at a site could predict the biomass of red and black-and-white colobus at four sites in Kibale. Although our sample size was too small for robust, statistical analyses, our results suggested that colobus biomass was related positively to the average protein to fiber ratio of mature leaves across sites. Most remarkably, when we accounted for food quality in this manner, the low population density at Dura River was no longer an anomalous outlier. It thus appears that, although food is abundant at Dura River, it is of low quality, and this is likely the reason that the site does not support a large colobus population.

While these studies suggest that the protein to fiber ratio of available foods may limit the size of folivore populations, we felt that the data was insufficient to convince managers to use these principles in constructing management plans. We felt that we needed several independent populations to increase our sample size and to develop a more rigorous predictive model. To do this, we turned to a series of forest fragments outside of Kibale. These forest fragments vary in size and composition, and provide a quasi-experimental setting that allowed us to investigate the influence of this ecological variation on primate populations. Before making any comparisons across fragments, we wanted to establish which populations were stable. If some populations were not at carrying capacity due to recent effects of disease, habitat loss, or hunting, then correlations between food availability and/or quality and folivore biomass could be spurious. In 1995, we surveyed the primate communities in 20 of these forest fragments to determine the abundance of black-and-white colobus monkeys. In 2000 and 2003, we resurveyed these fragments to assess population and forest stability, and to compare monkey biomass to the protein to fiber ratio of leaves in those fragments that we determined to have stable populations (Chapman *et al*., 2004).

We discovered that 3 of the 20 fragments inhabited by primates in 1995 had been cleared, and resident primate populations were no longer present. These fragments had remained intact since at least the 1940s, but recent economic conditions had led to more rapid deforestation. Most fragments had been cleared for charcoal production, gin-brewing, brick-making, or timber extraction. In the remaining fragments, the total black-and-white colobus populations had declined by 40% in just 5 years. While we had initially hoped that most colobus populations in the fragments would be stable, we found that there were only five stable populations. Although this was alarming from a conservation perspective, these five sites increased our sample size sufficiently to conduct a more robust statistical analysis of the protein to fiber model. Across these five fragments, colobus biomass was correlated with the protein to fiber ratio ($r^2 = 0.730$, $P = 0.033$). To examine the model more rigorously, we

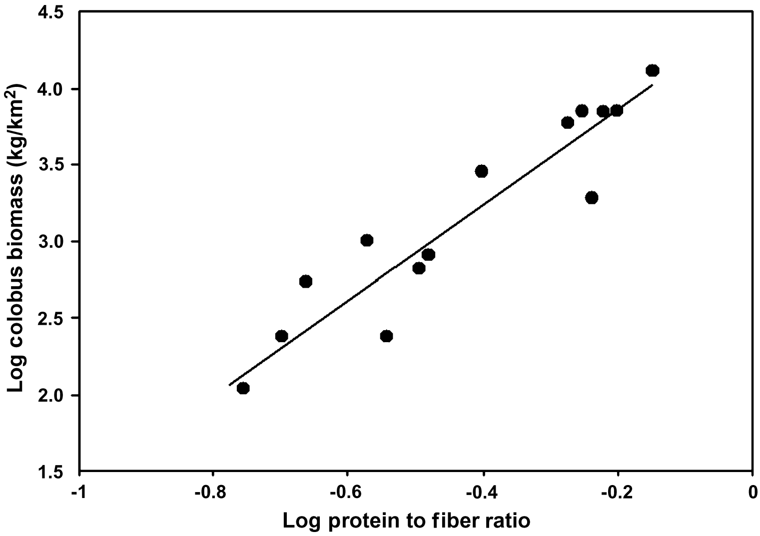

Fig. 6.1. The relationship between mature leaf chemistry and colobine biomass at rainforest sites in Africa and Asia.

combined the data from the fragments with the four sites from within Kibale and five published values from other sites in Africa and Asia. Colobine biomass across all 14 sites could be predicted with a significant level of confidence from the protein to fiber ratios of available mature leaves ($r^2 = 0.869$, $P < 0.001$; Fig. 6.1).

While the mechanism behind this correlation is not well understood, these results suggest that, if managers could provide colobus with foods high in protein and low in fiber, their populations would flourish. Studies such as this provide managers with alternative approaches for conservation. In the past, managers typically have promoted an animal species by removing threats; however, now the opportunity exists to plan to augment populations by providing high quality foods.

RESTORATION OF A PLANT COMMUNITY CONDUCIVE TO PROMOTING RED COLOBUS ABUNDANCE

This research only addressed half of what we wished to understand; we still needed to gain an understanding of how we could facilitate forest regeneration in such a way as to promote a forest that would support high red colobus abundance. An understanding of forest restoration processes could be very important for Uganda and Kibale, in particular. First, as economic situations change in Uganda and other African countries, we feel that there will be increasing interest in forest restoration. This may be encouraged by repercussions of the Kyoto Protocol. When industrialized countries fail to meet their commitments to reduce carbon omissions as they agreed to in the Kyoto Protocol, it is likely that they will turn to promoting reforestation in tropical countries, like Uganda, as a means of offsetting their carbon debt. This is already seen in activities of the FACE Foundation in Kibale and Mt. Elgon National Parks. Uganda can lead African countries in efforts of this nature. We say this because the Ugandan Government has made remarkable steps towards economic growth, while at the same time developing multifaceted environmental protection schemes. Thus, the economic growth that has occurred in Uganda over the last decade has been balanced, at least in part, by measures to protect the environment. These measures are formalized in the Constitution of Uganda (1995), the National Environment Statute (1995), the Wildlife Statute (1996), and the creation of the National Environment Management Authority (NEMA), to mention just a few. Furthermore, Protected Areas currently account for 14% of Uganda's total land area (Howard *et al*., 2000). As a result, Uganda has the potential to become an African leader in biodiversity conservation and environmental policy.

Second, understanding restoration processes is vital for Kibale given its history. As early as 1971, illegal destruction and encroachment occurred in the southern half of Kibale. In 1976, some 30 eviction orders were issued, but were never carried out. In 1983, the government again ordered settlers out of these encroached areas, and by 1984, it was estimated that 60% of the forest plots and 30% of the grassland plots had been abandoned. However, the situation soon reverted to the prior state and encroachment increased. On April 1, 1992, the government ordered settlers off the land and resettled all encroachers. Estimates of the number of people residing in the southern corridor vary dramatically. Based on aerial surveys counting houses, van Orsdol (1986) estimated that 8800 people were living in the southern corridor. A national census carried out in 1980 indicated that as many as 17 000 people were residing in Kibale. Baranga (1991) estimated 40 000 people, MISR (1989) reported some 60 000 people, and after the resettlement the National Environmental Management Authority (1997) estimated that 30 000 households, or approximately 170 000 people, were residing in Kibale. Whichever estimate one chooses, it is evident that a large number of people were residing in the southern corridor, and as a result forest was cleared and degraded. Understanding processes of forest restoration will aid in the management of this area.

To provide the Ugandan Wildlife Authority with an understanding of how they could facilitate forest regeneration to promote a forest that would support high red colobus abundance, we conducted a 4-year study to evaluate regeneration of indigenous trees 10 years after the pine plantations had been harvested. Further, since initial regeneration rates appeared slow, we conducted an enrichment planting experiment in an area of the harvested plantation and quantified the value of this planting program to enhance regeneration.

Pine plantations were established in Kibale between 1953 and 1977 on areas that were previously forested lands. These lands had been cultivated by agriculturalists, but abandoned when rinderpest devastated the livestock populations in the area in the early 1900s. Once the plantation matured, native tree species and shrubs invaded the understory and these were not removed by the plantation managers. With Kibale becoming National Park, management plans changed, the plantation was harvested and the areas were left to regenerate to native forest. The Kanyawara plantation was harvested between March 1995 and April 1996 and the area was left to regenerate.

Two 200 × 100 m (2 ha) plots were established in the harvested pine plantation and each was divided into 50 20 × 20 m sub-plots. In one plot (experimental), 400 seedlings of four species (*Albizia grandibracteata, Celtis africana, Celtis durandii,* and *Milletia dura,* 100 of each species) were planted. One of each of these species was planted in each 20 × 20 m subplot. These four species were selected because the seedlings were readily available, they often colonize disturbed areas, and these species have high protein/fiber ratio in the young leaves. The remaining plot was left as a control; however, a similar system of subplots was established to aid in quantifying regeneration and to ensure that each area received similar treatment by researchers. For each of the seedlings, saplings, and mature trees species in these plots, we determined the species identity and measured height, Diameter at Breast Height (DBH; if above 1.3 m), and Diameter at Ground Height (DGH).

A total of 44 tree species were found in the two areas, with 42 species in experimental plot, and 35 in control plot, and there was a great deal of overlap (80%) in species composition. The species that were not found in both plots were overall rare (maximum density 2 stems/ha). All tree species that were used as enrichment plant species in the experimental plots were encountered in higher numbers among the populations of the naturally regenerating trees in both plots. After 4 years naturally regenerating stems were much taller ($\bar{x} = 8.47$ m, $n = 1597$) than the planted seedlings ($\bar{x} = 0.5$ m, $n = 400$). The range of heights of planted seedlings (0.43–1.72 m) was much lower than the height of the naturally regenerating trees (0.2–15 m), and many of these seedlings are now under the canopy of trees that

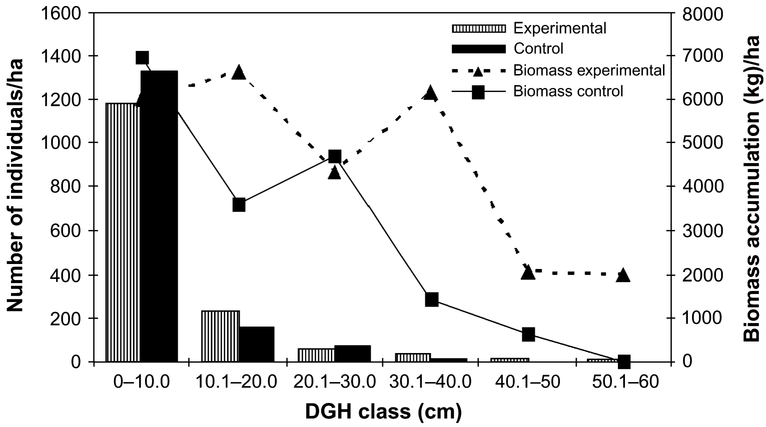

Fig. 6.2. Comparison of biomass accumulation among different DGH classes in experimental and control plots.

naturally regenerated. Counter to what was expected; the above ground biomass in the size classes of planted seedlings was greater in the control plot than in the experimental plot (Fig. 6.2).

Since the areas of Kibale that were grasslands in the 1960s and 1970s that were not converted to pine plantations are still largely fire-maintained grassland today, this study demonstrates that the use of fast-growing pine plantation species has facilitated the establishment and growth of indigenous tree species. However, this study also illustrates that, under these conditions, enrichment planting is not necessary for reforestation to progress at a reasonable rate.

The tree species that are regenerating naturally in these former pine plantations have leaves with higher protein to fiber ratios than found in the undisturbed forest. It is too soon to determine if the red colobus populations will increase with access to these regenerating areas containing these trees with high protein to fiber ratios; however, groups are frequently using these areas. We are monitoring the birth rates of groups that have access to these areas and groups that do not and we will soon have an experimental test of the prediction that access to foods high in protein and low in fiber will facilitate the growth of the endangered red colobus population.

DISCUSSION

The process outlined here could be coined *"Community Restoration"*, which we define as understanding determinants of animal abundance and plant community structure to such an extent that it is possible to modify the successional pathways of a plant community to arrive at a desired plant community structure for a set of animal species. We found no evidence in our study that there was a need for extra planting in our regenerating area; our goal of arriving at a desired plant community structure had been facilitated by the natural regeneration under pine plantations. In other cases, where regeneration is occurring from other forms of land conversion, supplementary planting may be a very effective tool, since we were able to see high survivorship in our seedlings. Supplementary planting may also be beneficial when attempting to manage for other types of animals (e.g., frugivores).

In Kibale it might be possible immediately to apply these notions to chimpanzees, since Balcomb *et al.* (2000) showed that chimpanzee density is related to the abundance of trees that produce large fruit and much is known about chimpanzee nutrition (Conklin-Brittain *et al.*, 1998). It is also possible that these concepts could be used in the opposite fashion, namely to push animals away from areas. For example, if tree species that were not eaten by elephants were planted in an area, once those trees matured, the area might be less attractive to herds than other areas (much is known about the nutritional requirement of Kibale's elephants (Rode *et al.*, 2006). Given the growth in Kibale's elephant population, the parks' increasingly isolated nature, and the damage that elephants do to the crops of the local communities (Naughton-Treves, 1998), this might be a long-term means of pushing elephants away from sensitive areas.

We expect that community restoration will be important for many tropical parks because many parks simultaneously contain areas of degraded forest and are attempting to protect endangered species that have limited geographical distributions. For Kibale, these questions are important because of the fire-maintained grasslands in the northern section of the park, degraded areas in the south, and endangered species of particular concern, like the red colobus and chimpanzees. With regards to the grasslands in the northern sectors of Kibale, evidence suggests that fire frequency is decreasing in these areas (J. Lwanga pers. comm.); and thus, this habitat is changing. In this case, it should be recognized that taking no active management is a management decision in itself – just as significant to the landscape and the animal populations it supports as managing for trees that promote the population of a particular endangered species. We say this because, if Kibale's grasslands are not managed, many locally endangered grassland-dependent species will decline.

An important aspect to remember is that the ability for tropical forest managers and conservation biologists to use community restoration as a management tool requires access to long-term data. Researchers need to monitor changes in animal populations and habitat over decades, not simply the 2–3 year duration of a major grant or the 1 year of a typical graduate research project. Managers need to realize that getting funding for long-term monitoring is extremely difficult; much more difficult than to get funding for a series of studies to test particular academic hypotheses. As a result, a great deal of the long-term data that will be useful to managers will only arise if the managers are patient with researchers who often appear to be only addressing a narrow academic question and encourage researchers to integrate long-term aspects or monitoring protocols into their programs.

Our research on red colobus and restoration started almost two decades ago. However, our impressions of Kibale were greatly influenced by publications and the stories of the researchers who preceded us, such as Tom Struhsaker, Gil Basuta, John Kasenene, and Jerry Lwanga. With the aid of Tom Struhsaker, Lauren Chapman and Colin Chapman will soon have a 40-year record of climate change, plant phenology cycles, plant nutritional changes, red colobus behavior, and primate population density and a 15-year data set on limnological patterns and regeneration. This illustrates that there is not only the need to encourage individuals to conduct long-term research, but there is a need to facilitate successive generations to keep working in specific areas. Such multi-generational research is facilitated greatly by the establishment and maintenance of long-term field sites.

SUMMARY

Human modification of ecosystems is threatening biodiversity on a global scale; effects are particularly severe in tropical rain forests where species diversity of many taxa is extraordinarily high. Closed-canopy tropical forest once covered 20% of the Uganda's land area, but deforestation has reduced this to just 3%. In this chapter, we reported on series of studies in Kibale National Park, Uganda to determine the critical factors that influence the abundance of endangered red colobus (*Procolobus rufomitratus*), and how we can facilitate forest regeneration in such a way to support high red colobus abundance. We found that the abundance of red colobus could be predicted by the protein to fiber ratio of available leaves, suggesting that managers could improve habitat quality for colobus by increasing the abundance of these foods. To explore the application of this idea, we conducted a 4-year study to evaluate regeneration of indigenous trees after a pine plantation had been harvested. Further, since

initial regeneration rates appeared slow, we conducted enrichment planting using species with high protein/fiber leaves in one area. Tree biomass in the regenerating area was substantial in comparison to the grasslands on which the plantation was established originally, indicating that the use of fast-growing pine plantation species has facilitated the establishment and growth of indigenous tree species. However, enrichment planting did not promote regeneration and was not necessary for reforestation to progress at a reasonable rate. While the tree species that are regenerating in these former pine plantations have leaves with high protein to fiber ratios, it is too soon to determine if the red colobus populations with access to these regenerating areas will increase as would be predicted by the model predicting colobus biomass from the availability of leaves with high protein/fiber ratios. Our research emphasizes that, for tropical forest managers to be able to use information on the determinants of animal abundance and plant community structure as a management tool, long-term data is required.

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