University of Alberta

Economics, biodiversity conservation, and sustainable development

by

RobiRobin Naidoo ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment
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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled *Economics, biodiversity conservation, and sustainable development* submitted by *Robin Naidoo* in partial fulfillment of the requirements for the degree of *Doctor of Philosophy.*

Martin Luckert

19 June 2003

Abstract

Conservation of biodiversity is considered a key component of sustainable development. Strategies to conserve the world's biodiversity have expanded from various extensions of ecological theory to embrace ideas from a broad array of disciplines. The inclusion of ideas from one of these fields, economics, has been controversial, and there is much disagreement on whether economic behaviour contributes to biodiversity conservation, or reduces the prospects thereof. I show here, through a combination of papers at both inter-country and local scales, that economic behaviour contributes to the loss of biodiversity in some instances, but may provide incentives for conservation in others. Rises in per-capita incomes cause country-level pressure on biodiversity to increase for most taxonomic groups, although birds show declining numbers of threatened species at higher income levels (Chapter 2). Recent country-level growth in per-capita income is correlated with liquidation of natural capital, as measured by clearing of original forest (Chapter 3). These large-scale results suggest that continued economic growth will exacerbate biodiversity loss, assuming that underlying mechanisms remain constant. At a local scale, I examined the linkages between avian biodiversity, nature tourism, land-use, and sustainable development at Mabira Forest Reserve, Uganda. Avian species richness and community composition are strongly influenced by land-use type, with subsistence agricultural areas harbouring few forest species (Chapter 4). Realistic levels of tree-planting are unlikely to lead to increased capacity for forest biodiversity conservation. On the other hand, an experimental assessment of tourist preferences for avian biodiversity showed that tourists are willing to pay increased entrance fees for the chance

to see higher numbers of birds (Chapter 5). This demand curve for biodiversity was combined with the opportunity costs of biodiversity conservation, based on deforestation patterns and current agricultural rents, to evaluate the potential for tourism to conserve the reserve's avifauna (Chapter 6). Current market conditions would conserve at most 114 of 143 species; this total would increase to 131 (~90%) if entrance fees were raised to revenue-maximising levels. This suggests that local "biodiversity markets" could play a positive role in conservation strategies.

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1. General Introduction

Prospects for sustainable development have been the subject of heated debate ever since the phrase was ushered into the public consciousness in 1987 (WCED 1987). The original definition as used in the Brundtland report was "development that meets the needs of the present without comprising the ability of future generations to meet their own needs"; however, various academic and popular interpretations of the term exist. To some, sustainable development is practically a given, since economic growth will lead to improvements in the quality of the environment through increased societal demand (Beckerman 1992, Lomborg 2001). Evidence for this point of view comes from a number of studies on the Environmental Kuznets Curve (EKC) hypothesis. The EKC hypothesis states that environmental degradation first increases as incomes increase, but at a certain point certain "turns" and beyond this decreases with increasing incomes (Rothman and de Bruyn 1998, Stern et al. 1996). Most of the empirical and theoretical work surrounding the EKC has been in the context of reversible measures of environmental quality, such as air pollution (Kauffmann et al. 1998). Its relevance to irreversible measures, such as the loss of species, or ecosystems that are beyond recovery thresholds, is less clear. Needless to say, there are strong differences of opinion amongst academics on the EKC hypothesis. These often fall along disciplinary or ideological lines (di Castri 2000), although Dasgupta (2002) attempts to reconcile viewpoints using the recent economics literature.

One aspect of the "sustainable" component of sustainable development concerns the conservation of biological diversity, or "biodiversity" (Wilson 1988). Biodiversity refers to the variety of life at all levels of organization, from genes through species to ecosystems and/or communities, and its conservation is a prime goal of the scientific discipline of conservation biology. Although its roots are firmly in the ecological sciences, conservation biology (or conservation science as those preferring more inclusivity call it; Western 2003) has begun to integrate concepts and methods from a variety of disciplines. For example, one of the earliest conservation biology textbooks devoted 24 of 25 chapters to material primarily biological in nature; the only exception was a philosophical chapter on inherent value (Soule 1986). Contrast this with a recent conservation text, in which over ¼ of the book's chapters deal with non-ecological aspects of conservation, including whole sections on valuing biodiversity and sustainable development (Primack 2002). In addition, today's pages of the discipline's flagship journal, *Conservation Biology*, are filled with growing numbers of articles emphasizing the importance of various social sciences such as political science (Song and M'Gonigle 2001), sociology (Thibault and Blaney 2001), and economics (Hughey et al. 2003). Clearly, strategies to conserve biodiversity have moved beyond extensions of ecological principles to encompass a broad, multidisciplinary approach.

With regard to the application of economics to biodiversity, much of the work in this area has surrounded measurement issues. Economists have been interested in determining how indices with appropriate weights can be developed for biodiversity (Solow et al. 1993, Weitzmann 1993), although Mainwaring (2001) has pointed out problems with attempting to reduce biodiversity measurements to a single index based on genetic similarity. Another area of recent research has been on the opportunity costs of biodiversity conservation (Ando et al. 1998). In the context of reserve design, economists have shown that building costs into reserve selection algorithms can significantly reduce the total expense of designing a network of reserves, while affording a similar level of species protection.

Valuation of the benefits of biodiversity (*i.e.*, the demand side of biodiversity) has not been as well-studied as the costs, especially in comparison to other ecosystem goods and services (Balmford et al. 2002, Godoy et al. 2000, Costanza et al. 1997, Kosz 1996). Despite a relatively large literature concerning human preferences for species attributes (Montgomery 2002, Kellert 1985) and for particular threatened species (Loomis and White 1996), we still have little idea of how people value more species versus fewer, both in the aggregate and for particular taxonomic groups. This area has particular relevance for policy decisions, given advances in measurement of the costs of biodiversity preservation (Balmford et al. 2003, Polasky et al. 2001, Ando et al. 1998). While a knowledge of the costs of preservation is invaluable in the design of conservation strategies, the demand for such strategies is also a key variable informing policy-makers of the public's willingness to pay for such programs. Unless biodiversity preservation is assumed to be a "first-trump" value (Randall 1991), evaluation of public preferences for tradeoffs involving biodiversity preservation is a key research area.

It is appropriate here to note that cross-disciplinary work encompassing both economics and biodiversity conservation has not been without controversy. For example, some natural scientists and philosophers believe that the existence of species should be considered outside the sphere of economic influence (O'Neill 1997), because species have an inherent right to existence and humans are therefore morally obliged to protect them. The implicit assumption here is that all species have a right to exist whatever the cost, but Randall (1991) has pointed out that other concerns may carry similar moral weight (i.e., the alleviation of chronic human poverty) but potentially conflict with biodiversity conservation. High-profile instances of economic valuation by teams primarily composed of ecologists (Pimentel et al. 1997, Costanza et al. 1997) have been heavily criticized for using a variety of inappropriate methods to produce values for ecosystems goods and services that are inflated and/or nonsensical (Bockstael et al. 2000, Freeman 1998). Authors of the studies have responded by saying that while the details of the studies can be quibbled with, the true value of the research is to show that ecosystem goods and services are extremely valuable and that they are not properly accounted for in our policy decisions (Costanza et al. 1998). Despite these arguments, collaboration between economists and conservation biologists is likely to increase, and there appears to be a general recognition from those working on biodiversity conservation that solutions will need insights from both disciplines (and others) to be successful (Daily and Ellison 2002, di Castri 2000).

In this thesis, I investigate instances where economic analysis can provide insight to problems involving the conservation of biodiversity. While each of the chapters is written as a stand-alone manuscript, the links among them are clearly visible. Chapters 2 and 3 deal with economic-biodiversity issues at the macro-scale, inter-country level, while chapters 4-6 describe an integrated ecological – economic project at a local scale.

Using secondary data, the second chapter describes a test of the EKC hypothesis, using the threat to, or pressure on, biodiversity, as a measure of environmental degradation. Relationships between per-capita income and the number of threatened species in a country were examined after correcting for other important factors. These are then interpreted in the context of the EKC hypothesis and research describing human preferences for species of various types.

The third chapter uses secondary data on natural capital, and asks what relationship exists between its liquidation and national economic growth rates. The context is the empirical economic growth literature, which has produced much research about the factors that affect how a country's economy grows, but has ignored the potential role of natural capital. The link between this chapter and others is that the measure of natural capital liquidation I use is conversion of forests to human-dominated habitat. Forests contain much of the world's biodiversity, hence liquidation of forests is likely to be correlated with biodiversity loss. In addition, the effects of forest conversion can be felt at different scales and in different ways: the second chapter deals with its effect on national economic growth rates, while the last chapter deals with its effects on economic returns from tourism at a local level.

Chapters 4-6 are a case study researching biodiversity, land-use, nature-based tourism, and sustainable development options at a tropical rainforest reserve in Uganda. Chapter 4 describes ecological work on avian biodiversity and community structure in three habitat types in and around the forest reserve. A particular focus here is on how an agroforestry scheme operating in the areas surrounding the reserve might affect the capacity of the area to function as a "buffer zone" in conserving forest biodiversity. Chapter 5 presents an experimental approach to assessing tourist preferences for avian biodiversity, in the context of protected area visitations. Chapter 6 integrates aspects of the research in Chapters 4-5 by examining both the opportunity costs and the demand for biodiversity at the forest reserve. A demand curve for avian species richness is constructed using models from Chapter 5, while the opportunity costs are based on the implied value of land prices, calculated through a GIS / spatial modelling analysis of deforestation at the reserve, and a species-area relationship for Ugandan forests that I develop from published data.

Finally, I discuss some general conclusions that can be drawn from this work in Chapter 7, and offer some thoughts on the prospects for sustainable development based on economic analyses of biodiversity conservation.

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2. Economic prosperity and threatened species[‡]

2.1. Introduction

Evidence suggests that the current global extinction spasm is resulting in the extermination of species at rates 100 to 1000 times greater than in pre-human times (Pimm et al. 1995). The main drivers of this event are hypothesized to be anthropogenic in origin: land conversion, global climate change, and the introduction of exotic species (Sala et al. 2000). Hypotheses concerning the nature of the relationship between biodiversity and various ecosystem services essential for human societies suggest that even from a utilitarian point of view, continuing to drive vast numbers of species to extinction may be an unwise course of action (Chapin et al. 2000, Tilman 2000, Daily 1997, Costanza et al. 1997). The cultural, aesthetic, and ethical reasons for avoiding a massive extinction of much of the earth's biodiversity have also been well-documented (Ludwig 2000, Gowdy 1997, Ehrlich and Ehrlich 1992). Therefore, why do species continue to be driven to extinction? A widely held view among those in the environmental sciences is that "economic growth", i.e., an increasing global population that desires an increasing per-capita level of consumption, fuels excessive land conversion, resource exploitation, and climate change (Sisk et al. 1994). As mentioned above, these are thought to be incompatible with conservation of biodiversity, and thus reduction of per-capita consumption (along with reduced population growth rates) is often a key recommendation in global conservation strategies (Mangel et al. 1996).

Interestingly, studies in the environmental economics and environmental policy literature have often come to a very different conclusion regarding the role of economic development and environmental degradation, namely that increasing per-capita income may be the only way that environmental problems will be solved (Beckerman 1992). It is thought that as per-capita incomes increase, the demand for environmental quality and the resources available for investment in the environment also rise (World Bank 1992). The relationship between per-capita income and measures of environmental degradation has been the source of much recent investigation. A lively debate has occurred regarding the

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[‡] A version of this chapter has been published. Naidoo, R., and W.L. Adamowicz. 2001. Effects of economic prosperity on numbers of threatened species. *Conservation Biology* 15:1021-1029.

hypothesis that this relationship is often an inverted-U shape; i.e., environmental degradation initially rises with increasing per-capita income, but at a certain income level subsequently declines. Evidence supporting this hypothesis, termed the Environmental Kuznets Curve (EKC), has been submitted for various types of air pollutants (Grossman and Krueger 1995, Selden and Song 1994, Shafik and Bandyopadhyay) and deforestation (Mather et al. 1999, Antle and Heidebrink 1995). However, others argue that there is no strong theoretical reason to expect the EKC to exist (Rothman and de Bruyn 1998, Arrow et al. 1995), and that previous studies that have supported the EKC have suffered from methodological and interpretation problems (de Bruyn et al. 1998, Stern et al. 1996). In addition, various other types of functional relationships have been shown to exist between measures of environmental degradation and per-capita income (de Bruyn et al. 1998).

To the extent that environmental quality is reflected in remaining levels of biodiversity, it is possible to examine the relationship between proxies for this variable and per-capita income. Since the majority of the world's biodiversity is concentrated in developing tropical countries (Wilson 1988), predicting the trajectory that biodiversity levels will take as per-capita income of these countries increases has important conservation implications. As part of the effort to catalogue species that have already gone extinct and those that are poised to do so, the World Conservation Union (IUCN) periodically publishes Red Lists of "threatened" animals and plants. These Red Lists, although far from a global species-by-species assessment, are a valuable source of information on the magnitude of the threat to any individual country's biodiversity. My goal in this paper was to examine, after controlling for confounding factors, the relationship between numbers of threatened species and per-capita income at the country level.

The hypothesis that increasing per-capita income results in increased demand for environmental quality assumes that people have adequate knowledge concerning the environmental good in question, or that at least enough information is provided to allow for the expression of these preferences. This may not be the case for threatened species, as the academic community itself is only beginning to investigate how ecosystems may function better with elevated levels of biodiversity (Chapin et al. 2000). Furthermore, to the extent that preferences may be expressed for threatened species, they may vary depending on what type of organism is threatened. In general, people tend to display preferences for species that are large, highly visible, and capable of displaying various behaviors interpretable as human-like (Metrick and Weitzman 1996, Kellert 1985). Indeed, several studies on threatened species have shown that conservation efforts have been motivated less by the degree of threat to a particular species, and more by whether the species belonged to a particular charismatic taxonomic group (Metrick and Weitzman 1996, Simon et al. 1995). It is therefore possible that the relationship between numbers of threatened species and per-capita income will vary depending on taxonomic status. Accordingly, I broadly classified threatened species into several taxonomic groupings, and analyzed per-capita income relationships separately for each group. Because mechanisms that may drive the EKC are poorly understood, I focus on the "stylized facts" arising from the relationships I examine, and the interpretations that arise from these exploratory analyses.

2.2. Methods

I used data from a recent report that examined the status of the global environment (World Resources Institute 1999). Data contained in this report are also available free at http://www.wri.org/wri/facts/data_tables.html. This publication contains, among other things, information on biodiversity, land-use, and economic activity for 157 countries. The World Resources Institute collates these data from various sources. Information on species endangerment, total species number, endemic species, protected areas, and forest cover comes primarily from the World Conservation Monitoring Centre (WCMC: http://www.wcmc.org.uk), which maintains extensive databases on threatened species and habitats throughout the world, and the IUCN Red Lists of Threatened Animals and Plants (IUCN 1997, IUCN 1996). Information on country area and land-use is collated from the FAOSTAT Statistics Database of the Food and Agriculture Organization of the United Nations (http://apps.fao.org/cgi_bin/nph_db.pl).

Consistent with IUCN classification, I considered the number of threatened species in a country to be the sum of all species in the Critically Endangered, Endangered, and Vulnerable categories. Threatened species were divided into 7 groups: plants, mammals, birds, amphibians, reptiles, fish, and invertebrates. Analyses were performed separately for each group. Criteria for consideration of threatened species status by the IUCN varied by taxonomic group. For marine species, only those that return to land to breed or nest are assigned to a country record. Threatened cetaceans were not assigned to particular countries, except for inshore or coastal species. Only vascular plants were considered by the IUCN when developing the list of threatened plant species. For birds, threatened species were listed for countries included within their breeding or wintering range. Threatened marine turtles were excluded from reptile totals, and most threatened marine fish were similarly excluded from fish totals. For invertebrates, no distinction appeared to have been made in the WCMC database between countries that had no threatened species and countries for which no estimate existed. Therefore for this group, I used in the analysis only those countries that had at least one threatened species. All known bird and mammal species were assessed for the 1996 Red List of Threatened Animals (IUCN 1996), whereas coverage for the other taxonomic groups, in particular invertebrates, was less complete.

In developing regression models for the effects of per-capita income on threatened species, I also included variables that account for country specific differences in ecology, level of human activity, and geography. The variables included those that potentially influence species endangerment through sheer species numbers or species-area relationships ("covariates"), land-use practices, and economic well-being (Table 2-1). Covariates included the total number of species (by taxonomic group) that occurred in a country, number of endemic species that occurred in a country (by taxonomic group), and country area. Most cetaceans were excluded by WCMC from total mammal species lists. Only breeding birds were considered by WCMC when compiling total bird species lists. Only flowering plants were listed in total plant species lists. Data were unavailable for invertebrates. Number of endemic species refers to the number of species that occur exclusively within one country's borders. For plants, all vascular plants were included by WCMC. Data were unavailable for fish and invertebrates.

I included three land-use variables that should influence numbers of threatened species. The first was the percentage of a country under domestication, which is a crude indicator of the degree to which national landscapes have been modified by agricultural use. It is defined as the sum of cropland and permanent pasture FAO land-use categories. It does not include developed lands or plantation forests. The second land-use variable was percentage of original forest cover remaining in a country, where original forest cover refers to the area of land that would have been covered by closed forest about 8000 years ago (assuming current climatic conditions), before large-scale disturbance by human society began. These were WCMC estimates based on global and regional biogeographic maps. Remaining forest is current forest area measured at some point within the last 10 years, depending on the country. The final land-use variable was percentage of a country in IUCN protected areas, where IUCN protected area is the sum of natural areas at least 1,000 ha in size in IUCN management categories I-V (generally described as scientific reserves, national/provincial parks, natural monuments, wildlife sanctuaries/managed nature reserves, and protected landscapes).

Finally, I included two economic variables in my analyses. I used per-capita Gross National Product (GNP) as a proxy for per-capita income of a country. Per-capita GNP refers to the total value of the final output of goods and services produced by the domestic economy as well as net income from abroad (1995 U.S. $), divided by the population. I also included the square of per-capita GNP as a quadratic variable in the analysis, in order to allow a range of possible nonlinear functional responses (see below).

Because the response variables were not continuous, but rather counts (non-negative integers), I used count data regression (Cameron and Trivedi 1998) instead of ordinary least squares regression in my analyses. Specifically, I used a negative binomial regression model, which has the following form:

$$\text{prob}\ (Y = y_i,\ \epsilon_i) = \frac{e^{-\mu_i(\epsilon_i)}[\mu_i(\epsilon_i)]^{y_i}}{y_i!} \qquad (1)$$

and

$$\ln \mu_i(\epsilon_i) = \mathbf{x}_i\beta' + \epsilon_i \qquad (2)$$

where Y is a random variable, y_i is the number of occurrences of threatened species, μ_i is the mean intensity parameter, $\mathbf{x}_i$ is the vector of independent regressors, β' is the vector of regressor coefficients, and e^{ϵ_i} is the gamma distribution with mean 1.0 and variance α, a measure of the dispersion of the data.

I used negative binomial models because the dispersion parameter was statistically significant in all models, indicating that a Poisson count data model would not be appropriate (Cameron and Trivedi 1998). I first attempted to fit models using the untransformed independent variables listed above. However, the fit of these models was poor, as indicated by extremely low deviance-R^2 and chi-square values, as well as by asymmetry and outlying observations in plots of residuals versus fitted values (Cameron and Trivedi 1998). Inspection of the independent variables revealed highly skewed distributions. I therefore log-transformed all the independent variables (with the exception of the $[\log(\mathrm{GNP})]^2$ variable) and used these transformed variables in subsequent analyses. Initially, I estimated models with all six noneconomic explanatory variables and the two per-capita GNP variables. I subsequently removed all noneconomic variables for which the coefficient was not significantly different from 0 (as defined by a p value > 0.05) and re-estimated reduced models.

Examination of the residual plots for these models revealed outlying observations for several taxa. In particular, the United States and Australia were outliers for four and three of the seven taxa, respectively. Both of these countries are wealthy industrialized nations that seem to have invested more into documenting the natural history of their fauna and flora than other countries in the analysis (with the possible exception of the U.K.). Accordingly, to remove any potential bias due to these countries, I removed them from the statistical analyses. Outliers in models for amphibians (South Africa, Japan), fish (Mexico), and invertebrates (South Africa) were also removed. The results of analyses with and without these outlier countries were qualitatively similar in most cases. Finally, to allow nonlinear responses in the noneconomic variables, I repeated the analytical procedures described above while adding to the models the squared terms of each of the original covariate and land-use variables. An extension to these analyses would be to use a systems approach to estimate the regression coefficients (Srivastava and Giles 1987), however this would be challenging, given the number of equations and the count nature of the data.

I interpreted the functional response of numbers of threatened species to the log of per-capita GNP by examining the sign and magnitude of the coefficients on both economic variables. The quadratic functional form I employ allows for nonlinearity in the relationships between income and threatened species. The Environmental Kuznets Curve hypothesis would be supported by positive linear and negative quadratic terms, but other relationships, including increasing numbers of threatened species as income increases, can be captured by this functional form.

2.3. Results

Results from three regression analyses (all countries, outliers removed, nonlinear effects of noneconomic variables) were similar in terms of responses of threatened species to the log of per-capita GNP (Table 2-2). When all countries were included in the analysis, income variables were significant predictors in all taxonomic groups except for mammals. The number of threatened plants increased linearly with increasing log(GNP). The number of threatened amphibians, reptiles, fish, and invertebrates all had a negative log(GNP) term and a positive quadratic term, indicating a general U-shaped functional relationship. The number of threatened bird species exhibited an inverted-U relationship with increasing log(GNP) that is consistent with the Environmental Kuznets Curve. When outlying observations were removed, the results were much the same, the only difference being that numbers of threatened fish species were no longer affected by either of the income variables.

The analysis including squared terms of noneconomic variables produced slightly different threatened species-log(GNP) relationships. One of the main differences was that in this analysis, mammals showed an inverted-U relationship with increasing log(GNP). In contrast to the other two analyses, fish and invertebrates showed a positive linear relationship between numbers of threatened species and log(GNP).

Of the 21 regression models in the three different analyses, only two (both of them having threatened mammal species as the dependent variables) had as many as three significant noneconomic independent variables. Covariates (i.e., total species, endemic species, or country area) were significant in 17 of the 21 models. As expected, these were all positively related to numbers of threatened species. Land-use variables were significant in only 5 models. The number of threatened amphibians decreased with increasing percentage of protected country area (two analyses). The number of threatened invertebrate species increased with the percentage of a country's land under domestication (in two models).

Although deviance-R^2's were higher in the models including all countries than in those where outliers were removed, examination of residual plots showed that models with outliers removed had superior fits. With the exception of plants and reptiles, where the deviance-R^2's were about equal, models that had allowed for nonlinearity in noneconomic variables had lower deviance-R^2's than the models where outliers were removed. This is most likely due to the fact that fewer noneconomic variables were included in the reduced models. I consider the results of the analysis which excluded outlying countries and which did not consider nonlinearity in the noneconomic variables to be the most robust, and therefore focus discussion on these results (Figure 2-1).

2.4. Discussion

One could conclude from these results that if the trends I have documented are stable through time, the future prospects for global biodiversity are grim. It has been estimated that at least 50% of the world's biodiversity is contained in the world's moist tropical forests (Wilson 1988). Most of these forests are in developing countries. The goal of most development policies, particularly those of the World Bank (World Bank 1992), is to increase per-capita income of developing countries (roughly defined as low-income and middle-income economies that have an average per-capita GNP of less than $9,385 U.S. 1995: World Bank 1997) so that they reach industrialized nation levels. The analyses show that within the range of developed country per-capita GNP, threatened plants, amphibians, reptiles, and invertebrates all increase with increasing per-capita GNP (Figure 2-1). If these relationships hold, it appears that much of the world's biodiversity will be threatened with extinction should countries reach levels of consumption and economic activity equal to those of developed nations. However, for bird species (and in some cases for mammals) there appears to be evidence of increasing preference for environmental quality as income increases. The challenge is to understand why this relationship exists in the case of birds, and to assess whether knowledge of these mechanisms could be transferred to help conserve species in other taxa.

Three factors may interact to produce the types of relationships I have observed between per-capita income and numbers of threatened species: income elasticity, institutional designs, and biological characteristics. Income elasticity refers to the percentage change in the demand for a particular good with a unit percentage change in income. The EKC relationship may arise from environmental quality being a luxury good, meaning that as income increases, the demand for environmental quality increases at a rate greater than the increase in income. Explanations of the results in a manner consistent with income elasticity as the driving factor would require that increasing preferences for the preservation of birds as income rises be greater than that for other taxonomic groups, since birds were the only group to show a negative relationship between numbers of threatened species and per-capita GNP. In fact, an income elasticity explanation would suggest that bird species preservation is a luxury good, while preservation of other species does not have this characteristic. I could not find any empirical evidence regarding the relationship between income and preferences for species conservation.

There is, however, evidence to suggest that in wealthy countries birds receive greater conservation attention than other taxonomic groups, regardless of relative degrees of threat (Simon et al. 1995). Of the 10 endangered species in the United States on which the most money has been spent, seven are bird species, including the top three species (Bald Eagle, *Haliaeetus leucocephalus*, Northern Spotted Owl, *Strix occidentalis caurina*, and Florida Scrub-Jay *Aphelocoma coerulescens*). These seven bird species account for 40% of the total amount of money spent on endangered species by United States federal and state agencies from 1989 to 1991, $127.6 million (Metrick and Weitzman 1996). Loomis and White (1996) have summarized data from studies assessing the willingness to pay (WTP) for preservation of various threatened species. The average WTP value for avoiding the loss of threatened species was greater for birds than either mammals or fish. This was true of studies that measured annual WTP values ($31.51 U.S. 1993 for birds vs. $26.67 for mammals and $24.92 for fish) and those that measured lump-sum payments ($165.41 for birds vs. $79.87 for mammals and $15.19 for fish). In addition, people are generally most inclined to protect species that are large, aesthetically attractive, and most similar to human beings in terms of their capacity for feeling, thought, and pain (Metrick and Weitzman 1996, Kellert 1985). Birds display many of these qualities, while plants, amphibians, reptiles, and invertebrates, generally the antithesis of the charismatic megafauna that typify threatened birds, increase in extinction vulnerability with increasing economic prosperity.

Institutional and biological factors are also likely to be important determinants of the relationships I have discussed. For example, the evidence is mixed regarding whether species richness in different taxa coincide in a given geographic area (Gaston 2000, Lawton et al. 1998, Howard et al. 1998, Dobson et al. 1997). Therefore, habitat protection measures targeted at one species or one group of species may not necessarily conserve biodiversity in general, and so it is not surprising, from a biological point of view, that I have observed different functional responses among taxonomic groups. Certain institutions may also make conservation of birds less formidable than for other taxonomic groups. For example, while mammals are often considered charismatic megafauna, I found only weak evidence of a decline in threatened mammal species as per-capita income increased. Many mammals are relatively large, and require much larger tracts of undisturbed habitat than birds in order to maintain viable populations (e.g., Noss et al. 1996). These large pristine areas are becoming increasingly scarce in industrialized countries. In contrast to their aesthetic and cultural values, mammals, particularly large mammals, have also been vulnerable to the expansion of subsistence-oriented human economies for several reasons, including competition for resources, danger as predators, and value as food and clothing (Kellert 1985, Burghardt and Herzog 1980). Therefore, although preferences for mammal conservation may exist among certain segments of society, institutions that promote habitat loss and consumptive use of mammals may prevent effective conservation. Less obvious complications may also be acting to reduce conservation efficiency of other taxonomic groups.

Although only threatened bird species declined as per-capita income increased, such a relationship may occur at some point in the future for other taxonomic groups. This depends on the relationship between preference for species protection (as embodied by policy and other measures) and income or development. In the case of threatened plant species, which increased with per-capita GNP, the range of economic development of countries may not encompass the range required to display an EKC relationship; i.e., the income range may not have yet reached the "turning point". Whether preferences for conservation of these species will increase with income is uncertain, and will depend on the evolution of preferences with income, increasing relative scarcity of species, the ability of institutions to respond to changing preferences and scarcity, and other factors. In addition, many of the species now listed as threatened will eventually become extinct. Therefore, although listed species may decrease, the number of extant species will not increase, but rather decline. Extinction is irreversible, unlike other environmental responses that have shown EKC relationships with economic prosperity (i.e., pollutant emissions, forest cover).

Caution in interpreting these results is required, because of the nature of the data used in these analyses. Although these data are, to my knowledge, the best of their kind, several concerns regarding their quality and appropriateness for these types of analyses should be raised. Most studies looking for evidence of Kuznets curve relationships have used time series data spanning one or more decades for a set of countries (Koop and Tole 1999, Grossman and Krueger 1995, Selden and Song 1994). Unfortunately, data on biodiversity at the country level simply do not exist over these time scales for most countries. There is also the issue of discrepancy in knowledge and search effort among the various taxa used in these analyses. Undoubtedly, taxonomic groups such as birds and mammals are much better known than plants and invertebrates, and therefore are likely to receive greater effort at determining the status of known species and the discovery of new species (McKinney 1999). Discrepancies in knowledge and search effort are also likely to exist among countries. Developing countries clearly have fewer resources to devote to biodiversity monitoring than richer countries. Quantifying the amount of time and resources that individual countries devote to this task would strengthen these arguments. Finally, my analysis assumes that each country's wealth affects the environmental quality of the country. However, concern for endangered species within a country may arise from other (perhaps wealthier) countries, prompting investment in species protection by direct transfer or by indirect means. Such "spillover" effects have been observed in Kuznets curves for transboundary air pollution (Hauer & Runge, unpublished data) but would be difficult to assess for endangered species. However, these spillover effects, and their manifestation in global biodiversity conservation programs, may have significant impacts on conservation programs in less wealthy countries.

2.5. Conclusion

I have examined global, cross-sectional data on economic prosperity, threatened species, and various covariates to investigate the relationship between income and threatened species. The important issue arising from the results is that for some taxa (birds, and in a limited number of cases mammals) increasing economic wealth appears to result in increased protection for threatened species, or at least is associated with reductions in threatened species numbers. This is in contrast to the majority of taxa that do not have such a relationship with income. It is important to continue to assess why this relationship holds for bird species and not others, so that this knowledge can be applied to the conservation of other species as incomes increase. Anecdotal evidence suggests that the relationship for bird species may arise because of different preferences (income elasticities) for threatened birds as an indicator of environmental quality. This may suggest that the public's preference for some species is effective in fostering protection for those species, but that preferences for other "small and slimy" species have not yet been recognized. However, the underlying institutions associated with conservation of threatened bird species may also be more effective than institutions associated with other taxa. Also, biological factors may result in different levels of effectiveness of conservation efforts. The key issue is to assess the reasons for relative "success" in the conservation of threatened bird species and to apply such knowledge to conservation of threatened species in other taxa.

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2.7. Tables

Table 2-1. Descriptive statistics for threatened species, covariates, and land-use variables.

Variable	n	Mean	Median	SD	Min.	Max.
Threatened plant spp.	150	157.2	24.5	318.6	0	1845
Total plant spp.	126	6121	3337	8109	234	55000
Endemic plant spp.	98	1515	226.5	3297	1	18000
Threatened mammal spp.	157	16.0	11	17.2	1	128
Total mammal spp.	140	153.4	128	105.4	3	450
Endemic mammal spp.	145	12.2	1	31.6	0	206
Threatened bird spp.	157	15.1	9	18.9	0	104
Total bird spp.	144	407.4	297.5	313.2	20	1695
Endemic bird spp.	153	15.3	0	50.0	0	393
Threatened amphibian spp.	154	0.8	0	3.06	0	25
Total amphibian spp.	108	68.4	26.5	101.0	0	585
Endemic amphibian spp.	149	21.4	1	51.7	0	366
Threatened reptile spp.	154	4.6	3	5.72	0	37
Total reptile spp.	111	122.0	72	141.9	0	748
Endemic reptile spp.	147	27.3	2	73.7	0	628
Threatened fish spp.	157	5.7	1	14.1	0	123
Total fish spp.	77	140.7	79	169.7	3	822
Threatened invertebrate spp.	131	17.3	5	58.1	1	594
Country area (ha)	157	82774	23034	204467	61	168885
Percent country domesticated	157	41.5	43	21.6	1	86
Percent country in protected area	152	7.6	5.5	7.61	0	43.1
Percent original forest cover remaining	148	29.8	20	29.2	0	100
Per-capita GNP (U.S. 1995$)	144	5309	1365	8806	80	40630

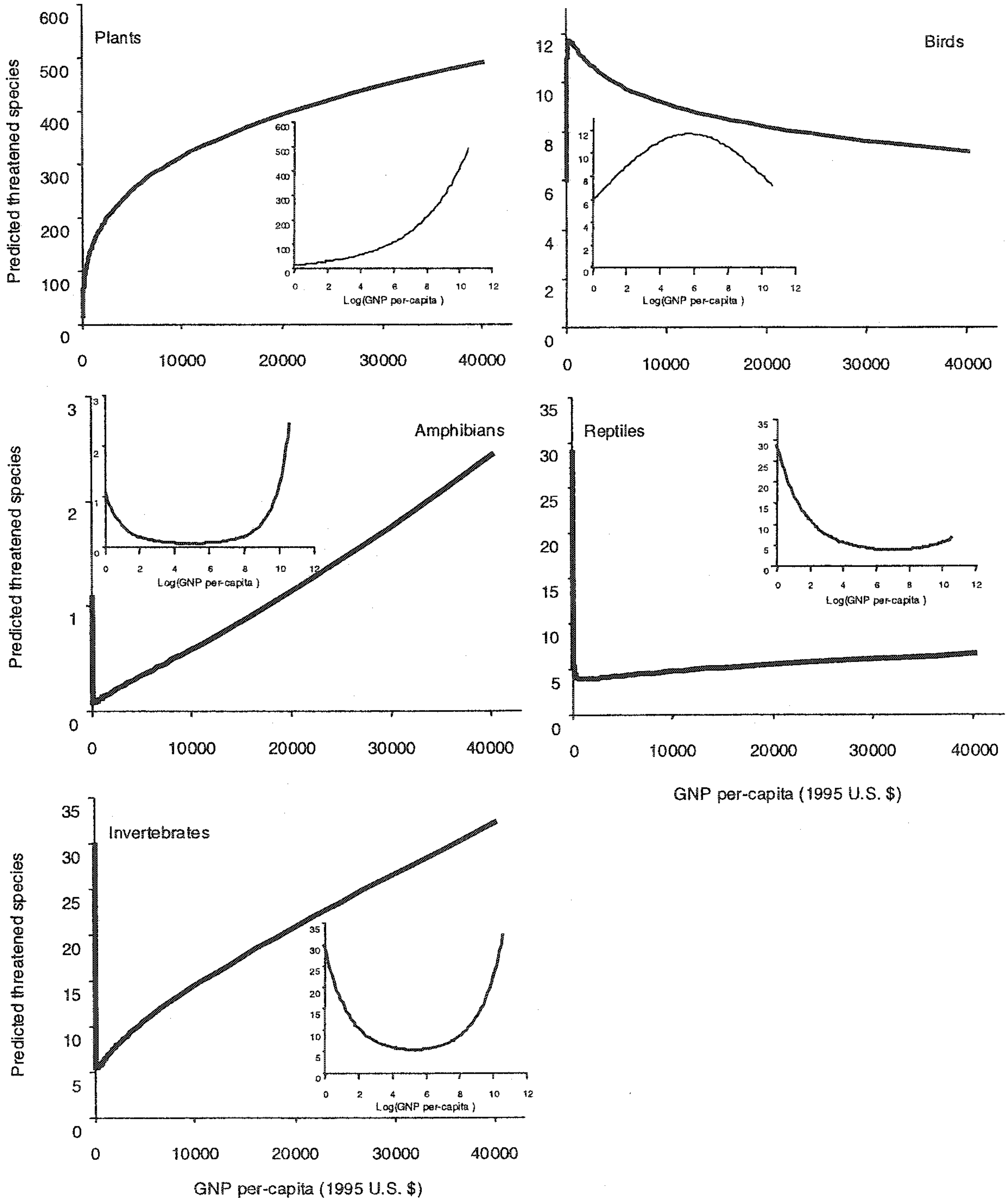
Table 2-2. Results of three count data regression analyses for the effects of per-capita income on threatened species of each taxonomic group, after controlling for confounding factors.

Independent variable	*Plants*	*Mammals*	*Birds*	*Amphibian*	*Reptiles*	*Fish*	*Invertebrate*
All countries							
log(no. spp.)	ns	0.27	ns	ns	0.85	0.78	-
log(no. endemic spp.)	0.53	0.33	0.37	0.74	ns	-	-
log(country area)	ns	0.79	0.14	ns	ns	ns	0.27
log(percent area domesticated)	ns	ns	ns	ns	ns	ns	0.45
log(percent area protected)	ns	ns	ns	-0.40	ns	ns	ns
log(percent original forest left)	ns	ns	ns	ns	ns	ns	ns
log(GNP per capita)	0.29	ns	0.24	-1.16	-0.63	-0.70	-0.95
[log(GNP per capita)]^2	ns	ns	-0.02	0.12	0.05	0.06	0.09
n	90	127	141	134	101	74	120
chi-square	13,223	61.3	285	14.1	32.5	529	1484
deviance R^2	0.61	0.84	0.74	0.74	0.67	0.50	0.70
p	<0.000	<0.00001	<0.00001	0.0002	<0.00001	<0.00001	<0.00001
Outliers removed							
log(no. spp.)	ns	0.28	ns	ns	0.82	0.71	-
log(no. endemic spp.)	0.52	0.33	0.38	0.72	ns	-	-
log(country area)	ns	0.08	0.15	ns	ns	ns	0.21
log(percent area domesticated)	ns	ns	ns	ns	ns	ns	0.38
log(percent area protected)	ns	ns	ns	-0.51	ns	ns	ns
log(percent original forest left)	ns	ns	ns	ns	ns	ns	ns
log(GNP per capita)	0.32	ns	0.23	-1.0	-0.57	ns	-0.65
[log(GNP per capita)]^2	ns	ns	-0.02	0.10	0.04	ns	0.06
n	88	125	139	130	99	72	118
chi-square	12381	59.6	263	67.1	31.8	487	1038
deviance R^2	0.52	0.84	0.74	0.65	0.61	0.26	0.26
p	<0.000	<0.00001	<0.00001	0.05	<0.00001	<0.00001	<0.00001
Nonlinearity in noneconomic variables							
log(no. spp.)	ns	ns	ns	ns	1.8	ns	ns
[log(no. spp.)]^2	ns	ns	ns	ns	ns	ns	ns
log(no. endemic spp.)	0.52	0.28	ns	0.71	ns	ns	ns

[log(no. endemic spp.)]^2	ns	ns	ns	ns	ns	ns	ns
log(country area)	ns	ns	ns	ns	ns	ns	ns
[log(country area)]^2	ns	ns	ns	ns	ns	ns	ns
log(percent area domesticated)	ns	ns	ns	ns	ns	ns	ns
[log(percent area	ns	ns	ns	ns	ns	ns	ns
log(percent area protected)	ns	ns	ns	ns	ns	ns	ns
[log(percent area protected)]^2	ns	ns	ns	ns	ns	ns	ns
log(percent original forest left)	ns	0.33	ns	ns	ns	ns	ns
[log(percent original forest	ns	-0.07	ns	ns	ns	ns	ns
log(GNP per capita)	0.32	0.59	0.62	-1.1	-1.3	0.38	0.36
[log(GNP per capita)]^2	ns	-0.05	-0.05	0.10	0.08	ns	ns
n	88	131	136	132	99	141	117
chi-square	12381	99.8	314	4.57	31.9	14.9	237
deviance R^2	0.52	0.79	0.14	0.41	0.62	0.02	0.14
p	<0.000	<0.00001	<0.00001	0.03	<0.00001	<0.00001	<0.00001

2.8. Figures

Figure 2-1. Predicted numbers of threatened species as per-capita GNP increases, using regression models developed with outlying countries removed. Significant covariate and land-use regressors (Table 2-2) were held at mean values, therefore predicted values do not reflect actual model predictions, but rather the qualitative functional response across the range of per-capita GNP's of countries included in the analysis. Inset graphs are plotted on a logged per-capita GNP scale; larger graphs are on a linear per-capita GNP scale.



3. Economic growth and liquidation of natural capital[‡]

3.1. Introduction

The world's natural capital (*i.e.*, biological resource stocks that provide flows of ecosystem goods and services; Daily 1997) is a valuable resource endowment that the human population depends on for existence. Curiously, for an item of such apparent high value, there is a remarkable divergence on viewpoints regarding sustainable use of natural capital, as noted by Dasgupta (2002). On the one hand, natural capital is often described as under increasing threat from expanding human economies (e.g., World Resources Institute 2000). Conversely, others claim that economic growth will result in environmental benefits (World Bank 1992, Beckerman 1992), or that the drawing-down of natural capital is not as severe as is generally portrayed (Lomborg 2001). Because increasing national per-capita incomes is a universal objective of national-level policies and development strategies (World Bank 2001b), expansion of the human enterprise will continue through the near future. It is therefore crucial to understand the relationship between economic growth and natural capital, so that informed decisions regarding sustainable development policy can be made.

The factors associated with economic growth have been the subject of much research, and theoretical models of economic growth have a long and venerable history (Solow 1956, Domar 1946). The compilation of large data sets consisting of a multitude of socioeconomic variables for many years and countries has led to the development of the empirical growth literature, in which researchers have tested long-held theories regarding the role of capital and labor in economic growth using country-level data (Sachs and Warner 1995a, Mankiw et al. 1992, Barro 1991). Syntheses of this literature have confirmed the positive effect of physical and human capital accumulation on growth, while also highlighting the importance of initial per-capita income, political freedoms, and economic openness to fast-growing economies (Sala-i-Martin 1997, Levine and Renelt 1992).

Despite much careful research in this field, there is remarkably little evidence

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regarding the relationship between natural capital and economic growth at the cross-country level (but see Sachs and Warner 1995b). Indeed, a recent literature review provided no discussion of natural capital; the words "environment" and "natural capital" were not mentioned in the text, and "natural resources" appeared in only one sentence (Temple 1999). Ignoring the role of natural capital in economic growth may be an outcome of its omission in earlier theoretical growth models (Solow 1956). Yet the divergence of views on a topic of such significance suggests that this is a serious oversight.

In this paper I assess the importance of natural capital to the economic growth of countries in the style of the empirical economic growth literature. I make an effort to use methods and data similar to those of the classic papers in this field, in order to maintain continuity, ensure comparability of results, and retain the legitimacy of accepted procedures. At the same time, the analyses presented here go beyond those that exist by including measures of natural capital liquidation in traditional growth regressions. As is common to most fields, the empirical economic growth literature is not without its flaws and detractors. Criticisms include the lack of a theoretical basis to regression models, the unwarranted assumption of a common growth process among countries, and endogeneity of explanatory variables. It is beyond the scope of this paper to provide a justification of the assumptions and methods of this field; readers are referred to Temple (1999) for a thorough review of both the positive and negative aspects of this research.

In Section 2, I provide a very brief overview of the theory behind empirical growth regressions. Section 3 of the paper describes the general methods used, the empirical data set, and some details of specification. In Section 4, results from economic growth models that include natural capital are presented, and a "core" model of explanatory variables is established. Subsequently, variables are added to this core model, including those representing scale and structure of the economy (Section 5), and geographical variables (Section 6). Section 7 concludes the paper with a review and discussion of the results.

3.2. Growth theory

Most papers in the empirical economic growth literature are loosely based on the Solow aggregate production function (Solow 1956), which specifies that capital and labour interact to determine changes in total output by means of a Cobb-Douglas production function,

$$Y = K^{\alpha}(AL)^{1-\alpha} \qquad [1]$$

where K is physical capital, L is labour, A is the level of technology, and α is the output elasticity of capital. Almost all papers in the field augment this original specification by adding human capital, H, to the aggregate production function,

$$Y = K^{\alpha}H^{\beta}(AL)^{1-\alpha-\beta} \qquad [2]$$

where β is the output elasticity of human capital. The addition of natural capital, N, as another aspect of capital's importance to output in the aggregate production function (with γ the output elasticity of natural capital), is easily accomplished within the Solow framework,

$$Y = K^{\alpha}H^{\beta}N^{\gamma}(AL)^{1-\alpha-\beta-\gamma} \qquad [3]$$

As has been mentioned, this aspect of capital has not been investigated in the present context. This twice-augmented growth function [3] thus includes two additional measures of capital, human and natural, along with the original physical capital measure of Solow, and forms the basic theoretical background for the work presented here.

In practice, most empirical growth studies have extended far beyond Solow's theory of economic growth, and have specified regression models that include numerous other variables in addition to those predicted by theory. Theoretically relevant variables such as the savings rate, population growth, and initial income are joined by a host of other variables, encompassing economics, politics, and trade. Many of these have been established as robust, significant explanators of growth. I follow this same, somewhat *ad hoc* procedure here; the next section reports on the specifications used in this paper.

3.3. Methods

I assessed the importance of natural capital to the economic growth, from 1960-1999, of over 70 countries using linear regression models. This was a cross-sectional analysis, i.e., each country had only one observation, rather than a series of observations over a number of years. These models included variables typical of past growth regression efforts, as well as an estimate of the level of liquidation of an important aspect of natural capital, forests. Forests provide a diverse array of ecological goods and services of benefit to humans (Daily 1997). They are also critically important to the conservation of biodiversity: one-half to two-thirds of all species on Earth are thought to live in forests (World Resources Institute 2000). Finally, they are among the most widely distributed of ecosystems, covering about one-third of the Earth's land surface (Noble and Dirzo 1997), thus permitting a detailed cross-country comparison. I use the term "liquidation" here because the conversion of land from forest to another land-use type results in at least a semi-permanent depletion of this stock of natural capital.

To properly assess the effect on economic growth of the amount of forest area that has been cleared in a country, it is necessary to control for several confounding area measurements. The fact that countries have different geographical areas must be accounted for, as must the area of forest that was initially present in a country. Without including these measurements of area, large countries with a small area of original forest cover would be analytically indistinguishable from small countries with a high percentage of their area originally covered by forests. I therefore specified country area, area originally covered by forests, and area of forest cleared, as separate explanatory variables in growth regressions. This specification also allows for the effects of all three of these variables on economic growth to be individually assessed.

Data

Data on economic growth of countries were obtained from World Development Indicators 2001 (World Bank 2001a)[1]. For each country, I fitted linear regressions to the 1960-1999 time series of the natural log of per-capita GDP (1995 U.S.$), and used the slope of these regressions as the measure of economic growth in each country over this time period. Many previous studies have used per-capita GDP in international dollars, and have not estimated growth trend, but rather used the start and end years of the time period in question to estimate economic growth. Both of these procedures have been criticized, and the method I used has been recommended by several authors (Temple 1999, Nuxoll 1994). Growth estimators using 1995 U.S.$ and international dollars are so highly correlated ($r = 0.88$, $n = 91$, $P < 0.0001$) that results are likely to be similar regardless of which is used, however GDP in international dollars is available for fewer countries and years.

Data on life expectancy in 1960 (a measure of initial human capital formation), average annual savings rate 1960-1999 (a measure of physical capital accumulation), per-capita GDP in 1960 (a proxy for initial per-capita income), and average annual population growth rate from 1960-1999 (crude proxy for growth of the labour force) were obtained from World Development Indicators 2001. Data on the average number of assassinations per year and average number of revolutions per year (measures of political stability) were obtained from the Global Development Network Growth Database[2]. These were averaged over the years 1960-1999, or in the case of countries missing data for certain years, over whatever subset of years was available. Data on number of years an economy has been open were obtained from the Harvard Centre for International Development[3]. Data on geographical area, countries' original forest cover, and remaining forest cover (at about the mid-1990's; estimate years vary slightly for countries) were obtained from the World Resources Institute[4].

Transformations/Outliers

Per-capita GDP in 1960, country area, area of original forest, area of forest cleared, and ratio of forest exports value to GDP (see below for description of this variable) were log-transformed to satisfy distributive assumptions of OLS regression analysis. Botswana and South Korea, two countries with extremely high economic growth rates, were removed from all analyses following statistical screening for outliers. These were the only two countries with growth values outside of 2.7 standard deviations from the mean (1.5 interquartile ranges), indicating significant deviance from the rest of the sample (Fox 1997). They were also the countries exerting the greatest degree of influence in preliminary regression analyses. Studentized residuals (Fox 1997) were 3.66 and 3.02 for Botswana and South Korea, respectively; no other country had an absolute value greater than 2.2. Cook's D-statistic (Fox 1997) for these two countries was also higher than any country remaining in the analysis, and was an order of magnitude greater than the nearest remaining country in the case of Botswana.

Three Sahelian countries with below-average growth rates (Burkina Faso, Chad, and Niger) were also removed from the analysis because their complete lack of original forest cover was overly influencing the partial relationship between area of forest cut and economic growth. Note that their effect was to *strengthen* the negative relationship between these two variables (a partial correlation of - 0.785 with these variables included, as opposed to – 0.652 without them), hence removing these three countries resulted in a more conservative estimate of the effect of natural capital on economic growth.

Economic scale/structure

The structure and level of development of a country's economy may affect the way in which forest conversion has influenced economic growth. The effect of forest clearance on economic growth in countries with large forestry sectors or very low per-capita incomes may be quite different from its effect in countries with small forestry sectors or high per-capita incomes. While economies of less-developed countries generally have larger natural resource and agriculture sectors than developed countries (Perkins et al. 2001), some richer countries with abundant forest resources have developed economies with a relatively high dependence on timber as an exportable commodity (e.g., Canada, Finland). To investigate these issues, I included two variables that code for the importance of the forest sector (the log-transformed ratio of forest product exports to total GDP), and economic development (dummy variable for less-developed countries). These two variables were interacted with the area of forest cleared, thus allowing for the effect of forest clearance on economic growth to vary accordingly.

Data on forest product exports were taken from the Food and Agricultural Organization of the United Nations[5]. The only year that these data overlapped with the economic growth time series was 1999, hence export data were from this year only. The dummy variable for less-developed countries refers to countries in World Bank income categories 1-3, i.e., those countries with an average per-capita income of less than $9,636 U.S. in 1996 (also referred to as developing, underdeveloped, or Third World countries).

Geographical effects

The influences of environmental variables such as land-use and geographical location of a country may be confounded with those of natural capital. Because forests are not uniformly distributed over the earth's surface, and because remaining forest area and agricultural land area may be inversely correlated, these factors should be accounted for in growth regressions using forest capital as an explanator. Accordingly, I obtained data on the area of domesticated land in a country[6], and also coded each country with a dummy variable to represent the region of the world in which it is located[7]. These variables were then added to regressions explaining economic growth based on economic correlates and forest capital variables.

3.4. Natural capital and economic growth

The empirical starting point was a regression including standard economic explanators, and variables used to assess the effect of forest clearance (Table 3-1, Model 1). While studies in the literature find a wide array of variables to be significant explanators of economic growth, the variables used in this initial regression model (excluding the natural capital variables) have been found robust to a wide variety of permutations in model specification, and are widely accepted as important to growth in cross-sectional studies (Temple 1999, Sala-i-Martin 1997). In this analysis, however, the coefficients on the number of assassinations per year, the number of revolutions per year, and average annual population growth from 1960-1999 were not significantly different from zero in the initial regression (Table 3-2, Model 1). All other variables in Model 1 were significant explanators of growth; their influences are discussed below with reference to Model 2 (Table 3-2). The regression model was highly significant ($F = 10.4$) and explained about 61% of the variance in national economic growth rates.

To more clearly examine the influence of natural capital depletion on economic growth, I removed non-significant variables from Model 1 and specified a reduced-form regression equation (Table 3-2, Model 2). I did, however, retain country area (non-significant in Model 1) in all reduced-form regression equations so that the forest area variables continued to be corrected for differences in country size across the sample[8]. The results from Model 2 (Table 3-2) show that proxies for initial human capital, physical capital accumulation, initial income, and economic openness were all highly significant explanators of economic growth in the expected direction. *T*-values ranged from 3.5 to 5.7 in absolute terms, well beyond the threshold for significance at the $P < 0.05$ level. The negative effect of initial income on growth is indicative of the "conditional convergence" effect, i.e., that other things held constant, poorer countries tend to grow faster than richer countries (Temple 1999, Sala-i-Martin 1997, Sachs and Warner 1995a, Mankiw et al. 1992, Barro 1991). Positive effects of physical capital, human capital, and an economy's openness on economic growth are robust findings consistent with previous reviews (Sala-i-Martin 1997). These results are therefore similar to those of earlier studies that used shorter time periods and various measures of economic growth.

In addition to these expected economic correlates, there was strong evidence that countries that liquidated their natural capital fastest had higher rates of economic growth than those with greater remaining levels (Table 3-2, Models 2). As mentioned, country area was not significant, therefore economic growth did not depend on the geographical size of a country, a result noted by (Reynolds 1985). Original forested area had a negative effect on growth in the reduced-form models, suggesting that countries with less original forest have grown faster than heavily-forested countries. Additionally, countries that had cleared more of their original forest have also grown faster than those with more original forest remaining (Figure 3-1). The standardized regression coefficient on this variable (0.546) fell within the range of those for the economic correlates (0.389 – 0.944 in absolute value), indicating an impact on economic growth of similar magnitude to these more commonly-held explanatory factors. These results suggest that natural capital does have an important effect on national economic growth rates, despite having received little attention in the empirical growth literature.

The regression equation of Model 2 was highly significant, with a higher F-value than Model 1 (F=14.6), and explained a similar amount of variance in economic growth (60%). I therefore take Model 2 to be the "core" model for sections that follow, in which the effects of various additional explanatory variables on the robustness of the natural capital relationships are assessed.

3.5. Natural capital, economic growth, and scale/structure of the economy

Model 3 of Table 3-2 shows the results of a regression including all variables of Model 2, as well as the logarithm of the importance of forest product exports, and a dummy variable for less-developed countries. The dummy variable was negative and marginally significant, providing weak evidence that less-developed countries grew more slowly than developed countries, after controlling for other variables. The majority of less-developed countries are located in the tropics, and others have postulated that these countries may grow more slowly because of the prevalence of virulent tropical diseases, erratic rainfall, and poor soils for agriculture (Perkins et al. 2001, Gallup and Sachs 1998). I address this geographical hypothesis on economic growth in more detail in Section 5. The forest exports variable was insignificant, suggesting no effect of the importance of forest product exports to the economy on economic growth. The direction, significance, and magnitude of the coefficients on all variables held over from Model 2, including those representing natural capital and its liquidation, were similar. The regression was also once again significant, explaining 60% of the variance in economic growth.

Next, I added interaction terms of the forest area cleared variable to the LDC dummy and the forest exports variable. The results are presented in Model 4 of Table 3-2. The LDC dummy variable, along with its interaction term, were this time not significant. These results thus provide no evidence to support the notion that poor, resource-rich countries rely more on natural capital depletion for economic growth than richer countries, as has been suggested (Sachs and Warner 1995b). However, the forest exports variable coefficient is now negative and marginally significant (Table 3-2, Model

3), suggesting that countries with a greater share of forest exports in their economies grew more slowly than those with a lesser share. Evidence that countries with a greater share of primary product exports grow more slowly than those countries with less of a dependence on natural resource exports has previously been provided by Sachs and Warner (1995b). The interaction between the importance of forest exports and area of forest cleared was positive and also marginally significant. This indicates that the effect of the area of forest cleared is conditional on the value of the forest exports variable, and vice-versa. Coefficients on the variables in Model 3 changed slightly from previous models, but their direction and significance as explanators of economic growth remained the same (marginally significant in the case of original forest cover). The regression equation of Model 4 was again highly significant (F-value of 10.8), and explained a greater share of the variance than Models 1 and 2 (67%).

An understanding of the effects of an interaction in a multiple regression model can be improved by calculating the regression coefficient of each variable at various levels of the other. Figure 3-2A shows the relationship between the coefficient on LNAREACUT and the value of LNFPDGDP, and Figure 3-2B the relationship between the coefficient on LNFPDGDP and the value of LNAREACUT. The coefficient on LNAREACUT is positive for values of LNFPDGDP above – 8.1 (Figure 3-2A). Since this is relatively close to the minimum value of LNFPDGDP (-10.7), the relationship between LNAREACUT and economic growth is positive over most values of forest export importance. The coefficient on LNFPDGDP is negative at most values below the mean of LNAREACUT (8.6), and positive at most values above (Figure 3-2B), indicating strong conditionality in its effect on economic growth.

Overall, results from Models 3 and 4 provide weak evidence for the following. For most countries, the effect of forest clearance on economic growth is positive. Only in countries with very low ratios of forest product exports to GDP will forest clearance have had a negative effect on growth. On the other hand, the direction of the effect of forest exports on economic growth is more strongly conditional on forest clearance: economic growth in countries with a greater-than-average area of forest cleared is positively affected by the increasing importance of forest exports in the economy, while the reverse is true in countries below the mean area of forest cleared. There is some evidence to indicate that developing countries may have grown more slowly than developed countries, but this is not a strong effect.

3.6. Natural capital, economic growth, and geography

A common problem in the empirical growth field is the uncertainty surrounding the regression specification, in terms of omitted variables, explanatory variables that may be correlated with unspecified variables actually driving a relationship, and reverse causality. By using variables for which both theoretical and empirical relationships with economic growth have already been demonstrated, I hope to have reduced the likelihood of these problems with the economic explanators. For the natural capital variables, however, it is possible that unspecified variables correlated with original forest cover and the area of forest cleared are actually driving economic growth. The direction of the relationship between economic growth and forest clearance is also an issue; increased economic growth may result in more forest cleared, not vice-versa.

One approach to addressing reverse causality problems involves the use of "instrument" variables (Hayashi 2000). In this approach, the independent variable of interest in the original regression model is regressed on a variable that is expected to be uncorrelated with the original dependent variable. The residuals of this regression are then used as an independent variable in the original regression model. There are many variables that are correlated with deforestation (Angelsen and Kaimowitz 1999), and hence many possible instruments for forest clearance. Variables such as the length of the road network and off-farm employment are strong correlates of deforestation (Angelsen and Kaimowitz 1999), and may not be as strongly related to economic growth as the explanators I have specified in the growth equations. However, because forest clearance has occurred at different times in different countries, appropriate instruments would need to be temporally coincident with forest clearance in a country. Since data on the timing of forest clearance in different countries is scarce or non-existent, the instrument variable approach is probably not feasible in this case.

I have attempted to address the concerns raised above in two ways. The first involves investigating the effects of land-use that may be correlated with liquidation of forest capital. Because decreasing the area of forest may result in an increase in land used for agricultural production, agricultural land area has obvious potential as an unobserved correlate of economic growth. To explore this possibility, I specified models (Table 3-2, Models 4 and 5) that include the logarithm of the area of a country under domestication. Model 4 replaces original forest cover and area of forest cover cleared with domesticated area, while Model 5 includes both forest variables and the area under domestication. In both models, the coefficient on LNDOMES was insignificant, indicating that this variable was unrelated to economic growth rates. The magnitude and significance of coefficients on the economic explanators did not change, while the country area variable remained insignificant. Both forest variables remained significant with the addition of LNDOMES in Model 5 (the strength of the relationship between forest area cleared and economic growth actually increased with this specification). Model 4 and Model 5 were significant regression models, explaining 60% and 62 % of the variance in economic growth, respectively. Results from these two models suggest that the area of forest cleared does not appear to be acting simply as the inverse of productive agricultural land, in its effect on economic growth.

As a second exploration of potential confounding factors, I assessed the role of geographical variables on economic growth models that included measures of natural capital liquidation. Because not all geographic regions on the earth's surface have equal suitabilities for forest ecosystems, forests and their depletion may just be surrogates for unobserved geographical effects that influence a country's potential for economic growth. For example, humid tropical African countries may be disadvantaged economically by virtue of their high prevalence of virulent diseases. But this area is also naturally heavily-forested, and includes the Congo basin, an area that retains much of its original forest cover (Myers 1992). Because sub-Saharan countries have grown very slowly in recent years, it might appear that a high degree of original forest cover and low forest clearance have led to low economic growth in these countries, whereas this may in fact be due to unobserved factors such as those mentioned above.

I attempted to control for such possibilities by adding dummy variables for geographic region to the regression equation of Model 2, and examining whether regions that had significantly higher or lower economic growth differed in their effect of natural capital liquidation on growth. Because of small sample sizes (less than 10 countries in each region), dummies for Eastern Europe and Central Asia, North America, South America, and Middle East and North Africa were excluded from the analysis. Model 7 of Table 3-3 shows the results of a regression model including economic, natural capital, and geographic variables. As with previous additions to the "core" model, the direction and significance of the economic and natural capital variables remain unchanged, although the area of forest cleared drops to marginally significant, with a t-value of 1.92, slightly below the $p < 0.05$ threshold of $t = 1.96$. The coefficient values on all variables remain similar to those in previous models. The regression was highly significant ($F = 12.2$), and explained 67% of the variance in economic growth.

Dummy variables for Sub-Saharan Africa and Latin America and the Caribbean were negative and significant, indicating that these regions had lower economic growth rates than others, after correcting for the rest of the explanatory variables. Both of these regions occur almost entirely within the tropics, and their component countries have low (in some cases extremely low) per-capita incomes. Slow economic growth has been noted in these regions before (Gallup and Sachs 1998). To determine whether the effect of natural capital liquidation was different for countries in these regions, I specified another regression model, that included variables from the core model, as well as the significant regional dummy variables and their interactions with the area of forest cleared variable (Model 8, Table 3-3). Neither of these interactions was significant, and indeed the significance of the dummy variables themselves disappeared in this model. However, all other economic and natural capital variables retained their significant effects on economic growth (marginally so for the number of years an economy has been open), with near-identical coefficient values for these explanators. This regression model explained 70% of the variance in economic growth, and was highly significant ($F = 13.7$). I conclude from this analysis that although evidence for geographical variation in growth rates is found in the lower growth of countries in Sub-Saharan Africa and Latin America and the Caribbean, these variables do not diminish the importance of natural capital liquidation on economic growth.

3.7. Conclusions

The negative consequences of forest clearance and logging to biodiversity conservation and ecosystem functioning have been well-documented (Siegert et al. 2001, Putz et al. 2001, Lawton et al. 1998). Forest ecosystems, particularly tropical forests, are thought to be the most speciose ecosystems on Earth (World Resources Institute 2000), and are also thought to play important roles in the regulation of watersheds and the global carbon cycle (Daily 1997). Recent attempts to calculate the economic value of standing forests have argued that conserving forests can have economic as well as environmental benefits (Kremen et al. 2000, Godoy et al. 2000, Adger et al. 1995). Economic valuation of such items as carbon storage, biodiversity option value, and ecotourism have emphasized that leaving an area under forest may have as much or more economic value as clearing it (Kremen et al. 2000, Chase et al. 1998, Adamowicz et al. 1996, Adger et al. 1995).

In contrast, this paper has shown that economic growth over a large cross-section of countries is generally accelerated by the clearance of forested areas. Using standard methods from the empirical growth field, I have demonstrated that economic growth rates of over 70 countries were affected by an original stock of natural capital and its subsequent liquidation. Countries that initially had a great deal of their surface area covered in forests have grown more slowly than those having fewer original forests. In addition, countries that have cleared large areas of their original forests have grown faster than those countries that retain much of their forested land.

These results are robust to many changes in model specification. Level of economic development, the area of land under domestication, and the geographical position of a country do not influence how forest clearance impacts economic growth, though each of these variables has their own effect on economic growth. The importance of forest exports to a country's economy did modify the impact of forest clearance on economic growth, but its main effect was to change the degree, and not the direction, of the relationship. Forest clearance was still a positive contributor to economic growth for most countries; only those countries having tiny levels of forest export importance were negatively influenced by forest clearance.

Forest clearance in countries has occurred at very different times throughout history; most of western Europe's forests were cleared many centuries ago (World Resources Institute 2000), whereas countries in the Amazon and Congo basins still retain much of their original forest cover (Myers 1992). For this reason, it is difficult to determine the reasons behind the relationship between natural capital and its liquidation, and national economic growth rates. To investigate this linkage more thoroughly, an ideal data set would be comprised of the variables utilized here, but over a time series dating to the time when countries first started large-scale clearance of their forests. Despite the lack of this information, I will speculate that countries have made productive investments from the dividends of the clearance of forests, and that these investments have contributed to growth from 1960 to 1999. For slow-growing natural assets such as forests, overexploitation and investment in alternative assets with faster growth potential is often the economically rational pathway (Clark 1973). The logic is thus that countries with more forests were disadvantaged because they needed to clear their forests so that more productive investments to the land under forests could be made. The earlier countries have started clearing forests, the greater the area has been cleared, resulting in a greater time for alternative assets to grow, and hence greater economic growth.

The results from this analysis are somewhat disconcerting from the point of view of sustainable development, as they suggest that liquidating one's natural capital will contribute to higher economic growth rates. If preservation of natural capital and continued economic growth are both policy goals, investment in substitutes to natural capital will be necessary. For example, the average growth rate of countries from 1960 to 1999 was 1.4 %/yr. Had initial life expectancy averaged 58 years instead of 53 and the average savings rate 21% instead of 18%, this same growth rate could have been achieved while clearing only 18% of original forest area, instead of the 56% that has actually been cut in the sample of countries used in this analysis. This example indicates that at a broad scale, investments in alternative types of capital can offset growth losses due to natural capital preservation. In the absence of such investments, the desire for sustained economic growth may lead to continuing liquidation of natural capital, with the attendant environmental consequences.

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3.9. Endnotes

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[1] World Development Indicators is a comprehensive publication that provides annual statistical indicators of economic development for over 150 countries.

[2] These variables are considered to be correlates of the level of economic freedom a country enjoys.. The World Bank's Global Development Network Growth Database contains time series data on macro- and micro-economic variables, as well as social indicators and fixed factors. Web address: Http://www.worldbank.org/research/growth/GDNdata.htm

[3] Http://www.cid.harvard.edu/ciddata/ciddata.html. This website contains datasets used i n publications by researchers affiliated with the Harvard Centre for International Development.

[4] Http://www.wri.org. Original forest cover is defined as the forest cover that would have been present in a country about 8000 years ago, before large-scale conversion by human societies occurred, assuming current climate conditions. Estimates were developed by the World Conservation Monitoring Centre based on global and regional biogeographic maps.

[5] Http:///www.fao.org. The FAO's FAOSTAT database contains data on forestry activities at the national and regional levels. Forest products refers to all finished and unfinished products derived from trees, including pulp and paper, charcoal, fibreboard, roundwood, and many others.

[6] Domesticated land refers to land that is under either permanent pasture or crops. Data were obtained from the World Resources Institute: http://www.wri.org.

[7] Data are from the World Bank's Global Development Network Growth Database: Http://www.worldbank.org/research/growth/GDNdata.htm. Regions are East Asia and the Pacific (EAP), Eastern Europe and Central Asia (EECA), Middle East and North Africa (MENA), South America (SA), North America (NA), Sub-Saharan Africa (SSA), and Latin America and the Carribean (LAC).

[8] Some might argue that the logarithm of country area should be removed from the reduced-form regression equations, since it was insignificant in the full-form model. I re-ran Models 2, 3, and 4 of Table 1 without country area, and the results were nearly identical to those presented here.

3.10. Tables

Table 3-1. Continous variables used in regression models of national economic growth ($N = 77$)

Variable (units)	Abbreviation	Mean	Std Dev	Min	Max
Dependent variable					
Slope of ln (Per-capita GDP (1995 US$) time series, 1960 - 1999)	LOGSLOPE	0.014	0.016	-0.03	0.06
Independent variables					
Average no. assassinations per year	ASS	0.27	0.47	0	2.74
Average no. revolutions and coups per year	REV	0.20	0.24	0	1
Annual population growth rate (%)	POPGRWTH	1.98	0.93	0	3.5
Ln (Country area (km^2))	LNAREA	10.3	1.56	6.24	13.7
Ln (Original area (km^2) of forest)	LNORGAREA	9.14	2.43	5.63	13.2
Ln (Area (km^2) of original forest cut)	LNAREACUT	8.59	2.27	5.63	12.8
Life expectancy in 1960 (years)	LIFEEX60	53.2	12.8	31.6	73.4
Average savings rate 1960-99 (%)	SAV6099	17.9	9.06	1.24	46.8
Ln (per-capita GDP (1995 US$) in 1960)	LNGDPCAP60	7.06	1.45	4.58	10.2
No. years an economy has been open	YRSOPEN	12.7	14.5	0	43
Ln (Exports of forest products as a proportion of GDP) *	LNFDPGDP	-5.97	2.01	-10.7	-2.4
Ln (Area (km^2) of country domesticated) **	LNDOMES	9.13	1.69	4.7	13.1

* $N = 71$

** $N = 80$

Table 3-2. Regression coefficients (*t* -values beneath) for models of economic growth, 1960 – 1999, including natural capital, economic scale / structure, and land-use.

Variable	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
Intercept	0.013	0.0023	0.028	-0.021	0.012	-0.0005
	(0.89)	(0.85)	(1.52)	(-0.57)	(1.07)	(-0.041)
ASS	0.0015	—	—	—	—	—
	(0.52)					
REV	-0.0087	—	—	—	—	—
	(-1.33)					
POPGRWTH	-0.0014	—	—	—	—	—
	(-0.72)					
LNAREA	0.0016	0.0015	0.0016	0.0015	-0.0012	0.0016
	(1.17)	(1.10)	(1.15)	(1.11)	(-0.71)	(0.69)
LNORGFOR	-0.0058	-0.006	-0.0061	-0.0042	—	-0.0059
	(-2.70)	(-2.78)	(-2.62)	(-1.67)		(-2.34)
LNAREACUT	0.0055	0.0057	0.0053	0.0084	—	0.0070
	(2.70)	(2.81)	(2.49)	(2.42)		(2.98)
LIFEEX60	0.00089	0.00099	0.00095	0.0011	0.0010	0.00099
	(3.81)	(4.46)	(4.24)	(4.71)	(4.68)	(4.52)
SAV6099	0.00098	0.0010	0.0012	0.0012	0.00092	0.0011
	(5.29)	(5.66)	(6.25)	(6.24)	(5.50)	(5.91)
LOGGDP60	-0.011	-0.010	-0.012	-0.013	-0.011	-0.010

	(-5.43)	(-5.34)	(-5.67)	(-5.97)	(-5.76)	(-5.31)
YRSOPEN	0.00044	0.00042	0.00032	0.00031	0.00045	0.00039
	(3.36)	(3.42)	(2.45)	(2.37)	(3.77)	(3.19)
LDC	—	—	-0.0097	-0.028	—	—
			(-1.75)	(-1.49)		
LDC x LNAREACUT	—	—	—	0.0020	—	—
				(0.99)		
LNFPDGDP	—	—	8.2E-05	-0.0093	—	—
			(0.11)	(-1.93)		
LNFPDGDP x LNAREACUT	—	—	—	0.0010	—	—
				(1.96)		
LNDOMES	—	—	—	—	0.0017	-0.0014
					(1.08)	(-0.75)
N	77	77	71	71	80	75
F	10.4	14.6	12.2	10.8	18.2	13.5
R^2	0.61	0.60	0.64	0.67	0.60	0.62
Adjusted R^2	0.55	0.56	0.59	0.61	0.58	0.58

Table 3-3. Regression coefficients (*t*-values beneath) for models of economic growth, 1960-1999, including natural capital and geography variables.

Variable	Model 7	Model 8
Intercept	0.022	0.021
	(1.74)	(1.32)
LNAREA	0.0012	0.00059
	(0.92)	(0.49)
LNORGFOR	-0.0048	-0.0045
	(-2.22)	(-2.17)
LNAREACUT	0.0039	0.0043
	(1.92)	(2.06)
LIFEEX60	0.00065	0.00067
	(2.73)	(2.93)
SAV6099	0.00086	0.00091
	(4.85)	(5.40)
LOGGDP60	-0.0081	-0.0082
	(-4.07)	(-4.33)
YRSOPEN	0.00026	0.00022
	(2.06)	(1.83)
EAP	0.0042	—
	(0.92)	

WE	5.3E-05	—
	(0.010)	
SSA	-0.013	0.012
	(-3.04)	(0.68)
LAC	-0.0083	-0.027
	(-2.19)	(-1.68)
SSA x LNAREACUT	—	-0.003
		(-1.56)
LAC x LNAREACUT	—	0.0020
		(1.15)
N	77	77
F	12.2	13.7
R^2	0.67	0.70
Adjusted R^2	0.62	0.65

3.11. Figures

Figure 3-1. The partial association between economic growth and area of original forest cleared (ln transformed): $r = 0.66$, $N = 77$, $P = 0.0049$. Partial associations measure the correlation between an independent variable in a multiple regression and the dependent variable, having controlled for the effects of other independent variables in the model.

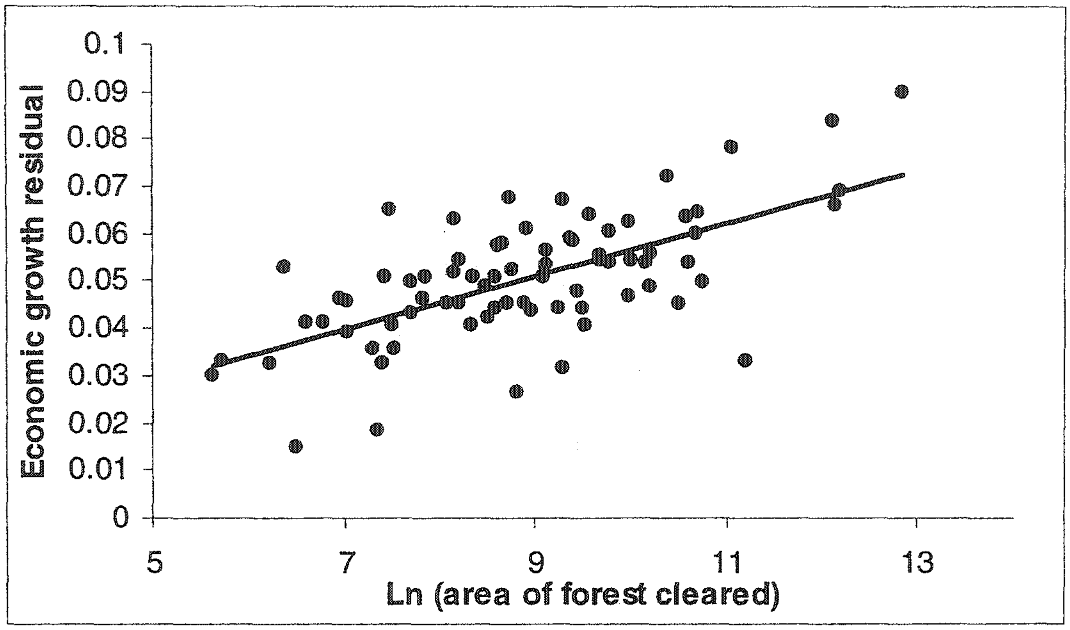
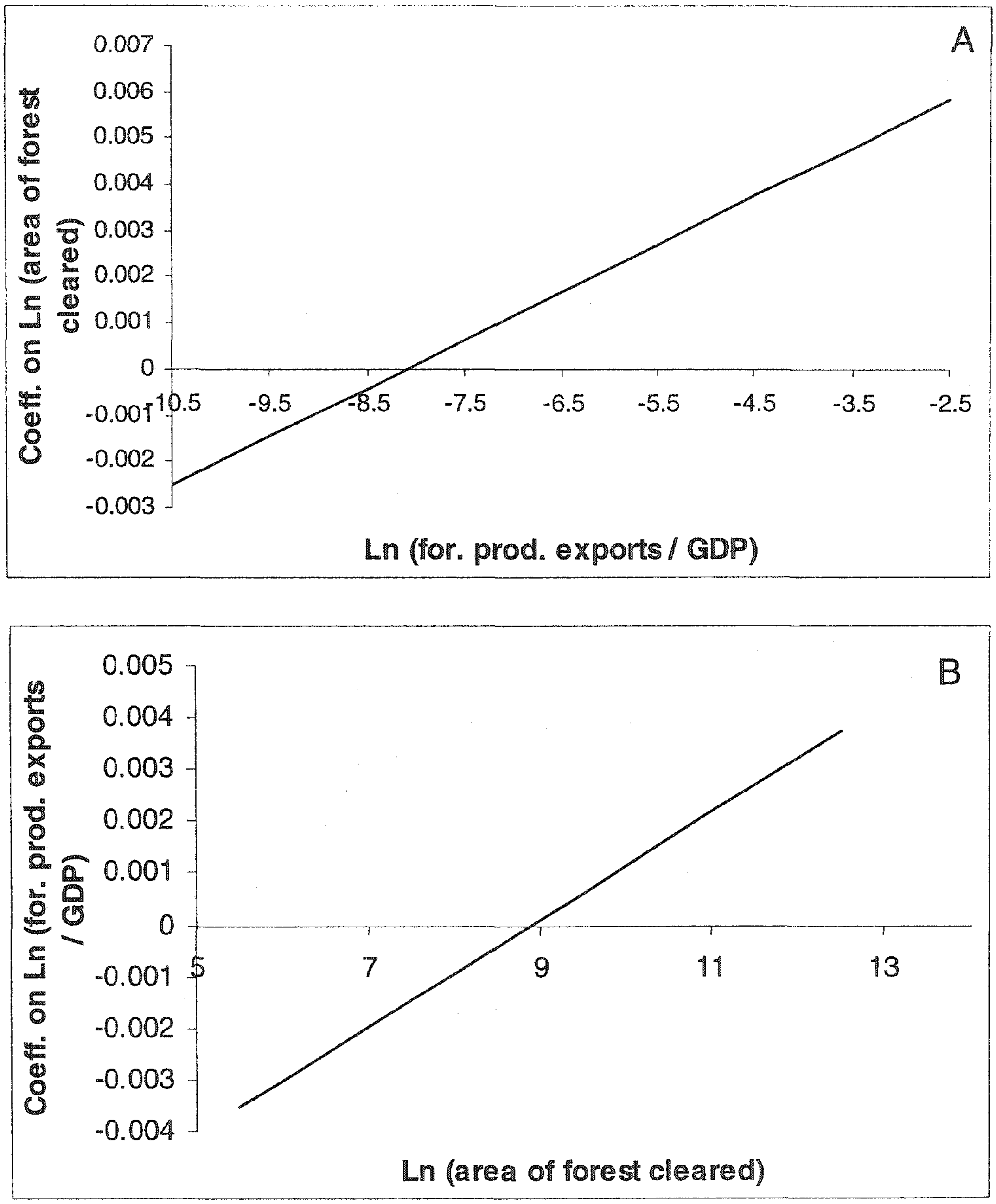


Figure 3-2. The interaction between area of forest cleared and the importance of forest exports, as represented by: (A) the relationship between the coefficient on ln (area of forest cleared) and ln (forest product exports / GDP) ; and (B) the relationship between the coefficient on ln (forest product exports / GDP) and ln (area of forest cleared).



4. Avian biodiversity in and around Mabira Forest, Uganda[‡]

4.1. Introduction

Land-use change is a key driver of current and future biodiversity change (Sala et al. 2000). In the tropics, conversion of native forests to pastures, croplands, and other human-dominated habitats is the primary cause of biodiversity loss (Myers 1992, Sala et al. 2000). Although population growth rates and rural poverty incidence are leveling off or decreasing in most areas of the tropics (World Bank 2001), human populations and absolute numbers of poor people will continue to increase in the near future, probably with concomitant increases in deforestation. However, other land-use dynamics also occur in the tropics. In areas that have been logged or cleared and then abandoned, regenerating secondary forest is a significant land cover type. The amount of secondary forest in the tropics is likely to increase in the future as logging activity increases dramatically (Laurance 1999). In addition, afforestation in smallholder agricultural areas (Place and Otsuka 2000) is an important land-use dynamic that has received little attention in the conservation literature. Smallholder agriculture (i.e., agriculture, often for subsistence, practiced by farmers on small pieces of land) can provide habitat for a variety of organisms normally associated with forest (Thiollay 1995, Perfecto and Vandermeer 2002), and hence may be an important component of landscape- or regional-level conservation strategies.

The effects of land-use dynamics and land cover types on tropical biodiversity are the subjects of a burgeoning literature. There has been a large amount of research on the responses of various elements of biodiversity to tropical deforestation, which emphasizes the negative effects of forest conversion to unsuitable human-dominated habitats (e.g., Myers 1992, Brooks et al. 1997, Castelletta et al. 2000). More recently, studies have assessed biodiversity in regenerating forest and/or agricultural areas as compared to undisturbed forest (Daily et al. 2001, Ricketts et al. 2001, Perfecto and Vandermeer 2002). Much of this work focuses on bird responses to such habitat modification. A review of this literature reveals no consistent relationships between avian species richness

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[‡] A version of this chapter has been submitted for publication. Naidoo, R. 2003. Avian species richness and community composition in a tropical forest – agricultural landscape. *Animal Conservation*, in review.

and forest age or condition. Studies variously show that primary forest contains more species (per sampling unit or unit area) than regenerating or disturbed forest (Bowman et al. 1990, Raman et al. 1998), fewer species (Johns 1991, Estrada et al. 1997, Dranzoa 1998, Blake and Loiselle 2001), or similar numbers of species (Andrade and Rubio-Torgler 1994, Warkentin et al. 1995, Plumptre 1997, Owiunji and Plumptre 1998, Thiollay 1999, Fjeldsa 1999). Studies that compare the avifauna between forested and agricultural areas of various types generally show that forested areas contain more species than agricultural areas (Blankespoor 1991, Ranjit Daniels et al. 1992, Thiollay 1995, Estrada et al. 1997, Pomeroy and Dranzoa 1997-1998, Daily et al. 2001). However, there is large variation among agricultural habitats in terms of their vegetational complexity, and therefore in their ability to harbor avian biodiversity (Thiollay 1995, Estrada et al. 1997, Wunderle 1999, Daily et al. 2001). Most research shows that species composition of avian communities differs among land-use types, but with varying magnitude. Some authors emphasize the dramatic shift from forest-interior species towards open or bushland species in regenerating, disturbed, or agricultural habitats (Johns 1991, Raman et al. 1998), while others note more optimistically that many forest species are found in habitats other than primary forest (Thiollay 1995, Gascon et al. 1999, Daily et al. 2001).

Agroforestry, i.e., the increased use of trees within agroecosystems (Winterbottom and Hazlewood 1987) has been touted as a means of both reducing pressure on contracting forests and raising the conservation potential of smallholder agricultural areas. By encouraging farmers to grow trees on their own land, degradation of adjacent woodlands and forests may be halted or even reversed (Murniati et al. 2001). More controversially, it has been suggested that agroforestry may enhance the suitability of agricultural areas for biodiversity conservation, to the extent that these areas may function as "buffer zones" between protected forest reserves and large-scale, intensive production areas (Gajaseni et al. 1996, Roberts et al. 2000, Cullen et al. 2001). Only a few studies, however, have assessed the degree to which agroforestry may actually contribute to the conservation of forest biodiversity (e.g., Perfecto et al. 1996, Roberts et al. 2000, Reitsma et al. 2001, Perfecto and Vandermeer 2002).

The aims of this study were to characterize avian species richness and community structure in forested versus smallholder agricultural land-uses, to estimate the capacity of current smallholder agricultural practices to support forest biodiversity, and to assess whether agroforestry programs may be capable of enhancing forest biodiversity in agricultural areas. The study was conducted in sub-Saharan Africa (Uganda), where population growth, deforestation, and rural poverty are acute problems likely to persist for the near future (World Bank 2001). An assessment of biodiversity in forested and smallholder agricultural areas, and the potential role of agroforestry in mitigating against forest biodiversity loss, is thus particularly critical in this region.

4.2. Methods

Study area

The study was conducted in and around the Mabira Forest Reserve (0°30' N, 32°55' E), a 300 km^2 remnant rainforest in southern Uganda (Figure 4-1). Tropical lowland moist forests once covered a large swathe on the northern shore of Lake Victoria in Uganda (Hamilton 1974). After centuries of deforestation, however, Mabira Forest is now the largest remaining forest in this region.

Because of its proximity to the capital Kampala, and to the country's second city Jinja, Mabira Forest exists in a zone of high human population density. The local residents are mostly smallholder farmers who cultivate a mix of cash and subsistence crops on small plots of land. Such crops include coffee, bananas, maize, cassava, ground nuts, and sweet potatoes; scattered trees are also present on farms. Although it is officially prohibited to reside, graze livestock, or cultivate land in the Reserve, violations are widespread (Howard et al. 2000, *personal observation*). Locals use the forest as a source of fuelwood, poles, construction material, wild fruit and vegetables, honey, fodder, and wild game (Mupada 1997).

Mabira Forest was seriously degraded in the 1970's and 1980's, and by 1988 about 25% of the forest had been converted to agricultural land, as the Ugandan government encouraged farmers to invade and settle in forest reserves (Mupada 1997). Following the government's decision to attempt stricter protection of its forests, settlers were ejected from these areas in 1988 and the forest was allowed to regenerate. The Reserve is now zoned into several different land-use categories, including Strict Nature Reserve (primary forest) and Ecotourism/Recreational (mostly secondary forest). The International Centre for Research in Agroforestry (ICRAF) has recently established a project with the Uganda Forest Department to encourage farmers to plant and maintain trees on farms adjacent to the forest, in an attempt to increase farm income while simultaneously reducing pressure on the forest and maintaining biodiversity.

Land-use types

I selected study sites in three land-use types in and around Mabira Forest Reserve: primary forest, secondary forest, and smallholder agriculture. Habitat types were identified from land-use maps and GIS coverages compiled by the Forest Department, and were verified by ground-truthing. Primary forest was located within the Nature Reserve zone of Mabira Forest Reserve and was characterized by relatively undisturbed forest that had not suffered any large-scale logging activity, although localized illegal pitsawing and snaring of wild game does occur. Secondary forest was located in the Ecotourism/Recreation zone of the Reserve and consisted of regenerating forest 13 years in age. This area is moderately impacted by fuelwood collection from local villagers. The smallholder agriculture area was outside the Reserve boundaries, in an area proposed as a "buffer zone" between more intensive agricultural areas further away from the forest and the Reserve itself.

Avian community censuses

In each land-use type, I placed between 30 and 35 count stations, separated by 150-250 m. Access was limited by poor road conditions in and around the reserve, therefore stations were placed along existing trails, footpaths, and motorable tracks in each habitat type. Differences in bird detectability between habitats influenced the choice of sampling protocol. Visual detections at sampling stations in dense tropical forest generally approach nil (Karr 1981), whereas in open agricultural habitats visual detectability is much greater. I therefore decided that the most efficient and equitable way of sampling birds in all three habitats would be to record sounds at each station for

15 minutes, and then identify vocalizations from the tapes. This procedure has been advocated for tropical avifauna surveys (Parker 1991), and can be a suitable (in some cases preferable) alternative to point counts in tropical rainforest habitat (Haselmayer and Quinn 2000).

Because breeding activity, and hence detectability, may vary with seasonality in Uganda, recording at each station occurred during two different time periods (Owiunji and Plumptre 1998). The first was the "wet" season in southern Uganda, during which recording was conducted from May 16 - May 26, 2001. The second was the "dry" season, during which recording was conducted from August 1 - August 7, 2001. For each sampling period, stations were visited within a three-hour period from sunrise (6:40 - 6:50) to 3 hours post-sunrise, on days with little or no wind and rain. At each station, an observer used a parabolic microphone and portable cassette recorder to record bird vocalizations for a 15 minute timed count. Observers changed direction every minute so that 360 degree coverage of the station was obtained. Based on field estimates of distance to singing birds, it appeared that all but the loudest birds were not recorded beyond a range of 75 m.

Species vocalizations were identified from tapes made at each station using personal knowledge and a reference CD set (Chappuis 2000). Those vocalizations that could not be identified using this procedure were sent to an expert ornithologist for identification (David Moyer, Wildlife Conservation Society, Tanzania).

Each identified species was assigned to a habitat guild based on Davenport et al. (1996) and Bennun et al. (1996). Forest specialists (FF) are characteristic of undisturbed forest interiors and are rarely seen outside such habitats. Forest generalists (F) may occur in both primary and secondary forest, as well as in forest strips, edges, and gaps, where they may be more common than in the interior of undisturbed forest. Forest visitors (f) are usually more common outside of forests, but may occasionally be recorded in forests. Open habitat specialists (O) are birds characterized by their preference for open woodland, bushland, and grassland. Relative abundances of each of these guilds in each land-use type were calculated by tabulating the number of species in each guild at each station. For a few species no guild could be assigned, due to lack of natural history information.

Local vegetation

Vegetation sampling protocols were adapted from several sources (Schemske and Brokaw 1981, Drapeau et al. 2000, Hobson and Bayne 2000). Vegetation structure was quantified by placing four 10 m x 10 m quadrats 25 m from each station, each at a 45-degree angle from the trail, such that there was one quadrat in the center of each of 4 quadrants of an imaginary circle of 50 m radius around the count station. Within each quadrat, every tree with a diameter at breast height (DBH) greater than 10 cm was measured for height and DBH. Within a 2 m x 2 m subplot in each quadrat, the number of woody stems between 1 and 10 cm DBH ("shrubs") was counted. Finally, a 10 m transect running across the quadrat was used to measure vertical foliage structure at various heights. At positions 1, 3, 5, 7, and 9 m along the transect, foliage touches along a real (0-3 m) or hypothetical (heights greater than 3 m) pole were scored at the following height classes: 0-0.5 m, 0.5-1 m, 1-1.5 m, 1.5-2 m, 2-3 m, 3-5 m, 5-10 m, 10-15 m, 15-20 m, 20-25 m, 25-30 m, and >30 m. Vegetation sampling was conducted from May 28 - June 16, 2001.

Landscape context

Count station coordinates (recorded using a handheld GPS) were entered into a GIS coverage of the study area. The GIS coverage was part of a nationwide land cover map derived from manual interpretation of SPOT XS satellite imagery from February 1989 to December 1992, as well as LANDSAT TM images and aerial photos from early 1995 (all at 1:50,000 resolution), and verified through extensive field surveying from 1993-1995 (Forest Department 2000). To determine whether landscape context influenced the species richness or community composition at count stations, the straight-line distance to the nearest primary, secondary, and agricultural edge was determined for each count station, using ArcView 8.1 (ESRI Systems, Redlands, CA). Although other studies have used the percentage of various habitat types within circles of varying radii around each station (Hannon 1999), count stations here were not far enough apart to allow such measurements to act as independent data points in analyses.

Statistical analyses

Avian species richness. - Because it was not possible to accurately determine the number of conspecific individuals at a station from the recorded vocalizations, inferences regarding species richness and community composition were drawn only from species presence-absence data. A species recorded during one or both of the two sampling periods was counted as being present at a station.

Species richness in each land-use type was estimated using the Jackknife-2 estimator (Colwell and Coddington 1994). Percent similarity of avifaunas among primary, secondary, and agricultural habitats was estimated using the Jaccard coefficient of similarity. Shannon's and Simpson's indices of diversity were also calculated for each land-use type (Magurran 1988).

Vegetation complexity. - Vegetation variables measured in each of the four quadrats per station were averaged to obtain a station-wide estimate. The standard deviations of these measures were included in the overall pool of vegetation variables as proxies of the heterogeneity in vegetational complexity at each count station. Density variables were the average number of trees per hectare and the average number of shrubs per hectare. Stem-specific variables were average DBH and average height of trees per station. The vertical foliage profile at each station was estimated by averaging foliage touches over all transect positions and quadrats for each height interval measured. A separate mean and standard deviation variable was therefore derived for the foliage "thickness" at each height interval from 0 to 30+ m. To reduce this large number of foliage variables, the first axis of a principal components analysis (PCA) was extracted and used in subsequent modeling efforts. This procedure was performed for all 96 stations, and also for each land-use type separately. In each case, the first axis explained 20 - 25 % of the variance, and can be interpreted as an axis of increasing foliage complexity, as the thickness at most foliage strata had strong positive loadings on it.

Bird-habitat relationships. - Species richness at count stations was modeled as a function of habitat using station-level vegetation variables and landscape distance-to-edge variables. A Generalized Linear Model (GLM) modeling framework was employed, with a Poisson distribution and log link function used to model species richness count data ("Poisson regression"). A stepwise regression procedure, using Mallow's Cp to select the next best-fitting variable and no further reduction in Akaike's Information Criteria as a stopping rule to determine the final number of variables entering the model, was used to find the best-fitting model (Mathsoft 1999). The number of species per count station was modeled over all stations, and also for each land-use type separately. Guild abundance (i.e., number of species of a particular guild per station) was also modeled as a function of vegetation and distance-to-edge variables, over all stations and for each land-use type separately. In a few cases, insufficient records of a guild in a certain habitat were available to run Poisson regressions. In these instances, a binomial distribution with a logit link function ("logistic regression") was used to model guild presence-absence at all stations.

Avian community structure and vegetation. - Comparisons of avian community structure among land-use types, and the influence of station-level vegetation structure, were assessed by various ordination measures. Correspondence Analysis (CA), Detrended Correspondence Analysis (DCA), and Canonical Correspondence Analysis (CCA) each have strengths and weaknesses, depending on the data collected and the specific goals of the analyses (Ter Braak 1986, Jongman et al. 1995, McCune 1997). The major characteristics of the avian community data and the vegetation data were revealed in similar ways by each analysis. I present here only the results of the DCA analysis, for several reasons. First, a strong arch effect (Jongman et al. 1995) was noted in scatterplots of the CA results, which the DCA removed. In addition, CCA incorporates environmental variables during the ordination itself (Jongman et al. 1995), whereas for my purposes I was interested in direct post-hoc comparisons of vegetation variables with avian community structure.

Ordination scatterplots in station-space and species-space were constructed to determine whether stations segregated according to land-use type and species segregated according to habitat guild. Pearson correlations of station-level vegetation variables with the DCA ordination scores were used to assess which vegetation characteristics were most important in structuring avian communities.

4.3. Results

Avian species richness

In total, 118 species from 35 families were recorded over two rounds of sampling at 96 count stations (Appendix A). Overall species richness and estimated species richness were highest in secondary forest (76 species recorded), followed by smallholder agriculture (66 species) and primary forest (58 species). At the station level, however, stations in primary forest and secondary forest had similar numbers of species and similar diversity index measures, while each of these were significantly lower at agricultural stations (Table 4-1). As measured by the Jaccard coefficient of similarity, primary and secondary forests were much more similar than either of these was to smallholder agriculture. A significant gradient from primary forest through secondary forest to smallholder agriculture was observed through abundance of species in different guilds (Table 4-2). Forest specialists were significantly more common in primary forest than either secondary forest or smallholder agriculture, while secondary forest also had more forest specialists than smallholder agriculture, where such species were virtually absent. The reverse of this was true for forest visitors, abundance being greatest at agricultural stations and lowest at primary forest stations. Forest generalists were more common in both forest types than in smallholder agriculture, while open-country specialists were significantly more abundant in smallholder agriculture than in either forest type.

Vegetation structure

Vegetation structure was significantly more complex in primary forest than in secondary forest, which in turn was much more complex than in smallholder agriculture (Table 4-3). Tree density, average DBH, and average height were all greatest in primary forest. Shrub density was greatest in secondary forest. Trees in agricultural areas were significantly fewer and shorter than those in forested areas, although their DBH was similar. There were also significantly fewer shrubs at agricultural stations than at primary or secondary forest stations. Foliage profiles of all three habitats (Figure 4-2) show that primary forest stations had the greatest foliage cover at most strata, although secondary forest stations had greater foliage cover from 3 – 5 m above ground level. Agricultural stations had much less cover at all height levels than either forest type.

Bird-habitat relationships

Best models of species richness based on vegetation and distance-to-edge variables varied widely among habitat types (Table 4-4). Station-level vegetation variables were significant predictors of species richness for all land-use types and most guilds. Some variables acted in different directions depending on the land-use type or guild (e.g., foliage complexity is positively related to species richness in secondary forest but negatively in smallholder agriculture). Generally, the explanatory power of models was highest in primary and secondary forest and lowest in agricultural areas.

Avian community structure and vegetation

DCA revealed a strong grouping of stations by land-use type (Figure 4-3). Primary forest and secondary forest stations cluster separately, yet show some overlap and are much closer to one another than to smallholder agriculture stations. The eigenvalue of the first axis was 0.637, indicating good separation (Jongman et al. 1995), and this first axis explained 23 % of the total variance in the avian community data set. The second DCA axis contributed little explanatory power to the data structure (eigenvalue 0.088, 3.2 % of the variance explained). An ordination plot of the species scores shows that species cluster according to habitat guild, although this clustering is not as tight as with stations (Figure 4-4). Forest specialists cluster to the far left of the diagram and open country species cluster to the right. Forest generalists and forest visitors show less grouping and are spread out between these two extremes (forest generalists more to the left-hand side and forest visitors more to the right).

Tree density was the vegetation variable most strongly correlated with the first DCA axis (Table 4-5). Many of the other vegetation variables were also strongly (negatively) correlated with this first axis, with lower axis scores thus corresponding to stations with heavy vegetation cover (but low variability). Few variables were significantly associated with the second axis, and its biological interpretation is unclear.

The relationship between tree density and the first DCA axis was best modeled by an exponential function, which explained 88 % of the variance (Figure 4-5, lower panel). Using this relationship, community scores on the first DCA axis can be predicted by tree density (Figure 4-5, upper panel). The effect on avian communities of potential increases in tree density resulting from agroforestry programs can therefore be projected (e.g., an increase from 52.4 to 200 trees/ha; Figure 4-5).

4.4. Discussion

Avian species richness

Assessing biodiversity levels in tropical landscapes is vital if we are to conserve a substantial number of species in developing countries with rapidly changing land-uses. Species richness (per unit area) in a landscape in southern Uganda was similar in primary and secondary forest, and lower in agricultural areas. This is consistent with previous results showing tropical forests to be more biodiversity-rich than nearby agricultural areas (Andrade and Rubio-Torgler 1994, Warkentin et al. 1995, Plumptre 1997, Owiunji and Plumptre 1998, Thiollay 1999, Fjeldsa 1999). Note that this is true only for species in the aggregate; species richness of open habitat specialists and forest visitors was far greater in agricultural habitats than in either forest type.

Within secondary forest, stations closest to a land-use edge (either primary forest or agriculture) had higher numbers of species than those further away from an edge. In particular, forest visitors were detected more frequently at secondary forest stations close to agricultural edges. Thus, high numbers of species in secondary forest may be related to penetration of species from adjacent habitats, a mechanism previously implicated in the high species richness found in tropical regenerating habitats (Dranzoa 1998, Blake and Loiselle 2001).

Secondary forest also had more variable vegetation structure than either primary forest or smallholder agriculture (coefficients of variability for tree density, average DBH and average height were all greater in secondary forest than in primary; Table 4-1). This variability means a greater variety of vegetation structures were present in secondary forest, thus supporting both forest visitors, which were more common at stations with a lower density of trees, and forest specialists, which were more abundant at stations with taller, thinner trees, greater foliage, and more uniform shrub cover.

Total species richness at primary forest stations was positively related to distance to the nearest secondary forest edge. This was because stations further away from secondary forest had greater numbers of forest specialist species than those closer to secondary forest. Increased abundances of forest interior species as distance from forest edge increases has been noted in a study of understory birds in another Ugandan forest (Dale et al. 2000). More generally, proximity to habitat edge has been shown to exert a strong influence on wildlife communities (e.g., Yahner 1988). Edge effects that may act to reduce the prevalence and abundance of forest interior species at ecotones include increased competition with more generalist species, increased predation and brood parasitism, microclimate modification, and reduction of food supply (Yahner 1988, McCollin 1998, Flaspohler et al. 2001).

Species richness at agricultural stations bore little relation to vegetation structure. Few significant models of guild species richness in agricultural areas were found, and these explained little of the observed deviance. The vegetation variables measured in this study may not be the most important factors influencing species richness in these areas. Other factors such as suitable nesting sites (Soderstrom and Part 2000), predation risk (Suhonen et al. 1994), and tolerance to human dwellings and activities (Mancke and Gavin 2000, Odell and Knight 2001) may be more important in limiting species persistence in simplified, human-dominated ecosystems such as the smallholder agriculture land-use. The few forest specialists found in the agricultural area were at stations very close to secondary forest. This is similar to results from tropical forests in central America, where forest bird abundance and species richness were highest in agroforestry areas adjacent to intact forest (Roberts et al. 2000, Reitsma et al. 2001).

Tree density was the only vegetation variable that was a significant predictor of the number of species per station across all stations. Increased tree density was associated with increased numbers of species, regardless of land-use type and habitat guild. This simple relationship is encouraging from a policy perspective, as it suggests that the best way to conserve high levels of avian biodiversity is to maintain or increases areas of high tree density. Protecting remaining primary forests (the land-use with the greatest density of trees) and increasing afforestation efforts in agricultural areas are therefore critical components of a biodiversity conservation strategy in this system.

Avian community structure

Land-use strongly influenced avian community structure, a non-surprising result given the plethora of studies that have demonstrated the dependence of bird communities on habitat type (Thiollay 1990, Drapeau et al. 2000, Schieck et al. 2000, Brawn et al. 2001, Pearman 2002). Community structure was somewhat different between primary forest and secondary forest, although this difference paled in comparison to that between either forest type and smallholder agriculture areas. While there was some overlap between avian communities of primary and secondary forest stations, agricultural station communities clustered very far away from forest stations (no agricultural station was within two 95% confidence ellipses of either primary forest or secondary forest). Stations in primary forest were characterized by high proportions of forest specialists and forest generalists, whereas agricultural stations were dominated by open habitat specialists and forest visitors. Secondary forest stations were somewhat intermediate between these two, although forest-dependent species were more prevalent than open specialists or forest visitors. These results clearly demonstrate that current smallholder agricultural practices in this system contribute little to supporting bird communities characteristic of tropical forests in the region.

A somewhat surprising result of this study was that secondary forest stations, while intermediate in community structure between smallholder agriculture stations and primary forest stations, were much closer in character to primary forest. After only 13 years, the avian community has shifted from a community (presumably) characteristic of open/bushland species to one that is close to a primary forest community. Other studies have documented the convergence of tropical avian communities along a chronosequence of regenerating sites (Bowman et al. 1990, Raman et al. 1998), and the convergence noted here is probably facilitated by proximity of relatively large tracts of primary forest. Nevertheless, these results are a promising sign that avian communities of regenerating secondary forest in southern Uganda may quickly return to communities characteristic of primary forest.

The community structure analysis reveals how more simplistic assessments of the avifauna may overestimate the potential for agricultural areas to contribute to forest biodiversity conservation strategies. For example, simply noting the presence-absence of forest bird species (forest specialists and forest generalists) in agricultural areas results in the conclusion that 33.8 % of the forest avifauna occurred in agricultural areas. Using a similar approach, Daily et al. (2001) recently cited a 29% occurrence of forest species in small-scale agricultural habitats as evidence of their high potential to contribute to forest bird conservation. Yet the community structure analysis I present here shows that bird communities in agricultural areas are entirely different from those found in forests. Applying simple presence-absence records of forest species in agricultural areas is thus a potentially misleading approach to assessing the suitability of agricultural habitats for forest biodiversity conservation strategies.

Agroforestry and forest bird conservation

The notion that agroforestry can result in "win-win" scenarios of increased biodiversity preservation, reduced farmer dependence on natural forests, and human welfare gains, has rarely been tested. While this study was not such an explicit test, the results do demonstrate a strong relationship between tree density and both species richness and community structure, over all land-uses. Any increases in tree density (e.g., from tree-planting due to agroforestry programs) are therefore predicted to lead to increased species richness, and a concomitant shift in community structure away from an open/bushland community and towards a forest community.

Because tree density is an easily-manipulated vegetation variable, quantitative predictions of the outcome of various policy decisions and agroforestry strategies can be made from the models in this study. For example, a four-fold increase in tree density in agricultural areas would shift avian community structure away from a community dominated by open habitat specialists to a community closer to those of secondary forest (see Figure 4-5), while at the same time modestly raising expected species richness per station from 18.9 to 19.5. Agroforestry programs in other areas of east Africa have more than doubled tree densities (Scherr 1995), thus such an increase is theoretically possible. However, increasing tree densities to 200-250 trees/ha in this system would likely compromise crop productivity on farms, making it unlikely that such a density increase would be managed for (J.-M. Boffa, ICRAF Uganda, *personal communication*). Doubling tree density to 100 trees/ha, still a substantial increase, would produce a small gain in expected species richness (to 19.1 species per station), but avian community composition would remain within the 95% confidence ellipse of current agricultural stations.

The potential of agroforestry programs to contribute to the conservation of forest bird community structure and composition, and for agroforestry areas to function as buffer zones between forested and intensive agricultural areas in southern Uganda, is therefore ecologically possible but economically infeasible, at present. Research documenting the effect of tree density on avian species richness and community structure in other tropical systems would lend further credence to the models and predictions presented in this paper. Because tree density is easy to measure, easy to manipulate, and straightforward to understand for both policy makers and rural landowners, its significance to tropical avifauna and other tropical taxa requires more quantitative research. Continued agroforestry research on minimizing tree-crop competition may produce combinations that will eventually allow ecologically-meaningful increases in tree densities. In the interim, encouraging forest regeneration on degraded or unused land is an efficient strategy to maintain or increase species diversity, and to quickly shift avian community structure towards forest specialist communities.

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4.6. Appendix 1

List of species recorded at count stations in Mabira Forest Reserve and surrounding agricultural areas. Guilds: FF = forest specialist; F = forest generalist; f = forest visitor; O = open habitat specialist.

		No stations present at in…				
Family	Species	Primary forest	Secondary forest	Smallholder agriculture	Total	Guild
Accipitridae	Melierax metabates	0	0	2	2	.
Alcedinidae	Halycon chelicuti	0	0	5	5	O
Alcedinidae	Halycon malimbica	17	6	2	25	F
Alcedinidae	Halycon senegalensis	0	1	0	1	O
Alcedinidae	Ispidina picta	0	0	1	1	f
Bucerotidae	Bycanistes subcylindricus	23	17	29	69	F
Bucerotidae	Tockus alboterminatus	0	2	12	14	f
Campephagidae	Campephaga quiscalina	3	4	0	7	FF
Capitonidae	Buccanodon duchaillui	8	8	0	16	FF
Capitonidae	Gymnobucco bonapartei	0	1	0	1	F
Capitonidae	Lybius bidentatus	0	0	16	16	f
Capitonidae	Lybius hirsutus	9	11	0	20	F
Capitonidae	Pogoniulus bilineatus	6	12	14	32	F
Capitonidae	Pogoniulus scolopaceus	29	22	15	66	F
Capitonidae	Pogoniulus subsulphureus	28	29	6	63	FF
Capitonidae	Trachylaemus purpuratus	21	18	0	39	F
Coliidae	Colius striatus	0	0	5	5	O
Columbidae	Aplopelia larvata	6	0	0	6	FF
Columbidae	Columba unicincta	4	3	0	7	FF
Columbidae	Streptopelia semitorquata	1	3	12	16	f
Columbidae	Treron australis	0	1	0	1	F
Columbidae	Turtur afer	0	1	16	17	f
Columbidae	Turtur tympanistra	6	7	1	14	F
Cuculidae	Centropus superciliosus	0	2	1	3	O
Cuculidae	Cercococcyx mechowi	9	6	0	15	FF
Cuculidae	Ceuthmochares aereus	1	0	0	1	F
Cuculidae	Chrysococcyx caprius	0	0	6	6	O
Cuculidae	Chrysococcyx cupreus	10	10	5	25	F
Cuculidae	Chrysococcyx klaas	2	9	6	17	f
Cuculidae	Cuculus solitarius	15	3	8	26	F
Dicruridae	Dicrurus modestus	0	1	0	1	F
Emberizidae	Emberiza flaviventris	0	0	4	4	.
Estrildidae	Lagonosticta rubricata	0	0	1	1	O
Estrildidae	Lagonosticta senegala	0	0	3	3	.

Estrildidae	Lonchura cucullata	0	0	8	8	O
Estrildidae	Nigrita canicapilla	7	11	23	41	F
Estrildidae	Spermophaga ruficapilla	0	1	0	1	F
Estrildidae	Uraeginthus bengalus	0	0	2	2	.
Fringillidae	Serinus citrellinoides	0	0	3	3	f
Fringillidae	Serinus mozambicus	0	0	16	16	.
Fringillidae	Serinus sulphuratus	0	0	1	1	O
Malaconotidae	Laniarius ferrugineus	0	2	0	2	f
Malaconotidae	Laniarius leucorhynchus	0	7	0	7	FF
Malaconotidae	Laniarius luehderi	1	0	0	1	F
Malaconotidae	Tchagra australis	0	0	3	3	O
Monarchidae	Elminia longicauda	0	0	4	4	f
Monarchidae	Terpsiphone rufiventer	19	1	0	20	FF
Monarchidae	Terpsiphone viridis	0	6	8	14	f
Muscicapidae	Muscicapa griseigularis	22	11	0	33	FF
Muscicapidae	Myioparus plumbeus	0	1	0	1	f
Musophagidae	Corythaeola cristata	3	8	3	14	F
Musophagidae	Crinifer zonurus	0	0	10	10	O
Nectariniidae	Anthreptes collaris	0	0	2	2	F
Nectariniidae	Nectarinia cuprea	0	0	7	7	f
Nectariniidae	Nectarinia erythrocerca	0	0	2	2	O
Nectariniidae	Nectarinia olivacea	7	6	1	14	FF
Nectariniidae	Nectarinia senegalensis	0	0	23	23	f
Nectariniidae	Nectarinia superba	0	3	0	3	F
Nectariniidae	Nectarinia venusta	0	0	3	3	f
Nectariniidae	Nectarinia verticalis	0	0	2	2	F
Numididae	Guttera edouardi	0	0	1	1	F
Oriolidae	Oriolus branchyrhynchus	35	9	0	44	F
Paridae	Parus leucomelas	0	1	12	13	f
Passeridae	Passer griseus	0	2	30	32	O
Phasianidae	Francolinus nahani	16	13	0	29	FF
Phoeniculidae	Phoeniculus castaneiceps	0	1	0	1	FF
Picidae	Campethera caroli	0	1	0	1	FF
Platysteiridae	Platysteira castanea	8	8	0	16	FF
Platysteiridae	Platysteira cyanea	0	2	27	29	f
Ploceidae	Malimbus rubricollis	0	2	0	2	FF
Ploceidae	Ploceus baglafecht	0	0	6	6	f
Ploceidae	Ploceus nigricollis	0	0	1	1	f
Ploceidae	Ploceus ocularis	0	0	3	3	f
Ploceidae	Ploceus tricolor	0	1	0	1	FF
Psittacidae	Psittacus erithacus	6	17	10	33	FF
Pycnonotidae	Andropadus curvirostris	15	10	0	25	FF

Pycnonotidae	Andropadus gracilirostris	7	0	0	7	FF
Pycnonotidae	Andropadus gracilis	1	0	0	1	FF
Pycnonotidae	Andropadus latirostris	30	20	0	50	F
Pycnonotidae	Andropadus virens	3	30	11	44	F
Pycnonotidae	Bleda eximia	1	1	0	2	FF
Pycnonotidae	Bleda syndactyla	0	1	0	1	FF
Pycnonotidae	Chlorocichla flavicollis	0	0	1	1	f
Pycnonotidae	Nicator chloris	21	13	0	34	F
Pycnonotidae	Phyllastrephus cabanisi	0	1	0	1	FF
Pycnonotidae	Phyllastrephus hypochloris	9	20	0	29	FF
Pycnonotidae	Phyllastrephus icterinus	15	15	0	30	FF
Pycnonotidae	Pycnonotus barbatus	1	28	31	60	f
Rallidae	Sarothrura pulchra	15	26	0	41	F
Sturnidae	Lamprotornis splendidus	1	0	3	4	F
Sylviidae	Apalis cinerea	3	0	0	3	FF
Sylviidae	Apalis rufogularis	1	0	0	1	FF
Sylviidae	Camaroptera brachyura	6	23	31	60	f
Sylviidae	Camaroptera chloronota	24	12	0	36	FF
Sylviidae	Camaroptera superciliaris	0	2	0	2	FF
Sylviidae	Chloropeta natalensis	0	0	11	11	O
Sylviidae	Cisticola erythrops	0	0	6	6	O
Sylviidae	Cisticola lateralis	0	0	7	7	O
Sylviidae	Eminia lepida	0	0	1	1	f
Sylviidae	Hylia prasina	30	22	4	56	F
Sylviidae	Macrosphenus concolor	25	7	0	32	FF
Sylviidae	Macrosphenus flavicans	13	12	2	27	FF
Sylviidae	Phylloscopus sibilatrix	17	15	1	33	F
Sylviidae	Prinia subflava	0	0	31	31	f
Sylviidae	Sylvietta virens	0	3	0	3	F
Timaliidae	Illadopsis albipectus	33	27	2	62	FF
Timaliidae	Illadopsis fulvescens	28	24	0	52	FF
Timaliidae	Illadopsis rufipennis	9	2	0	11	FF
Trogonidae	Apaloderma narina	6	0	0	6	F
Turdidae	Alethe diademata	0	4	0	4	FF
Turdidae	Cercotrichas leucophrys	0	0	2	2	.
Turdidae	Cossypha cyanocampter	4	7	1	12	F
Turdidae	Cossypha natalensis	0	1	2	3	F
Turdidae	Cossypha niveicapilla	2	3	4	9	F
Turdidae	Stiphrornis erythrothorax	21	13	0	34	FF
Turdidae	Stizorhina fraseri	35	22	0	57	FF
Turdidae	Turdus pelios	0	1	15	16	f
Zosteropidae	Zosterops senegalensis	0	4	31	35	f

4.7. Tables

Table 4-1. Comparisons of bird species richness and diversity among primary forest, secondary forest, and smallholder agriculture land-uses.

	Primary Forest	Secondary Forest	Agriculture
Species detected	58	76	66
Est. species richness*	68	95	80
% overlap with primary **	100	54	19
%overlap with secondary **	-	100	23
No. species per station (St Dev)	21.2^a (2.98)	22.5^a (4.20)	18.2^b (3.67)
H per station (St Dev)	3.04^a (0.141)	3.10^a (0.189)	2.88^b (0.201)
D' per station (St Dev)	0.95^a (0.007)	0.95^a (0.009)	0.94^b (0.012)

Superscripts indicate means that are significantly different (ANOVA, Tukey's HSD). H = Shannon index of diversity; D' = Simpson's index of diversity

*using Jacknife estimator to correct for undersampling of habitats (Colwell and Coddington 1994)

** Jaccard coefficient of similarity, multiplied by 100, where 0=complete dissimilarity and 100=identical

Table 4-2. Station-level species richness means for avian guilds in primary forest, secondary forest, and smallholder agriculture.

	Primary forest	Secondary forest	Agriculture
All species	21.2^{a} (2.98)	22.5^{a} (4.20)	18.2^{b} (3.67)
Forest specialists	11.5^{a} (2.11)	9.80^{b} (3.40)	0.35^{c} (0.66)
Forest generalists	9.06^{a} (1.86)	9.63^{a} (2.06)	4.23^{b} (1.98)
Forest visitors	0.60^{c} (0.60)	2.93^{b} (1.23)	9.65^{a} (1.66)
Open habitat species	0.00^{b} (0.00)	0.17^{b} (0.46)	3.13^{a} (1.41)

Superscripts denote significantly ($P < 0.05$) different means (ANOVA, Tukey's HSD)

Table 4-3. Comparisons of vegetation structure among primary forest, secondary forest, and smallholder agriculture.

	Primary forest	Secondary forest	Agriculture
Tree density (stems/ha)	725.7^{a} (154.6)	472.5^{b} (147.9)	52.4^{c} (59.3)
Average DBH (cm)	24.6^{a} (3.89)	21.5^{b} (4.32)	23.1^{a} (13.5)
Average height (m)	18.2^{a} (2.31)	13.4^{b} (2.03)	7.45^{c} (2.73)
Shrub density (stems/ha)	24,691^{a} (9879)	28,146^{a} (9419)	6,270^{b} (7385)

Figures are means (standard deviations).

Superscripts denote significantly ($P < 0.05$) different means (ANOVA, Tukey's HSD).

Table 4-4. GLM models of species richness using vegetation and distance-to-edge variables for various land-uses and avian guilds. Poisson regression is used when number of species per station is the dependent variable, and logistic regression when the dependent variable is presence-absence.

Dependent variable	Vegetation variable	Coefficient	Std. Error	*t*-value	% dev
All land-use types (n=96)					
No. species per station	Tree density (stems/ha)	0.0229	0.0073	3.13	13.2
Primary forest (n=35)					
No. species per station	Distance to nearest secondary forest (m)	7.72×10^{-5}	4.62×10^{-5}	1.67	19.6
No. forest specialist species per station	Distance to nearest secondary forest (m)	9.61×10^{-5}	6.27×10^{-5}	1.53	17.5
No. forest generalist species per station	Distance to nearest secondary forest (m)	1.86×10^{-4}	1.20×10^{-4}	1.55	22.2
	Distance to nearest smallholder agriculture (m)	-2.27×10^{-4}	1.38×10^{-4}	-1.64	
No. forest visitor species per station	Tree height (m)	-0.25	0.13	-1.88	31.7
	Tree density (stems/ha)	1.17	0.46	2.52	
Secondary forest (n=30)					
No. species per station	Variability in tree DBH	-0.046	0.027	-1.68	32.5
	Distance to nearest primary forest (m)	-5.98×10^{-4}	3.08×10^{-4}	-1.94	
	Distance to nearest agriculture (m)	-6.06×10^{-4}	4.09×10^{-4}	-1.48	
	First axis of foliage PCA	0.048	0.022	2.18	
No. forest specialist species per station	Average DBH (cm)	-0.06	0.027	-2.17	40.8
	Height (m)	0.045	0.021	2.16	
	Variability in shrub density	-0.034	0.019	-1.81	
	First axis of foliage PCA	0.052	0.028	1.86	

No. forest visitor species per station	Tree density (stems/ha)	-0.12	0.073	-1.58	34.1
	Distance to nearest smallholder agriculture (m)	-1.09×10^{-3}	7.23×10^{-4}	-1.51	
Agriculture (n=31)					
No. species per station	First axis of foliage PCA	-0.028	0.17	-1.63	12.2
No. forest generalist species per station	Shrub density (stems/ha)	-0.18	0.12	-1.50	17.7
	Variability in shrub density	0.13	0.08	1.70	
	First axis of foliage PCA	-0.069	0.04	-1.72	
Presence/absence of forest specialist species at stations	Distance to nearest secondary forest (m)	-5.41×10^{-3}	2.72×10^{-3}	-1.99	14.4

Table 4-5. Pearson correlations of vegetation variables with axis 1 and 2 from the Detrended Correspondence Analysis of the bird community data.

Vegetation variable	DCA1	DCA2
Tree density (stems/ha)	-0.89**	-0.11
Variability in % foliage cover 10-15m	-0.87**	0.02
% foliage cover 15-20m	-0.86**	-0.07
Tree height (m)	-0.84**	-0.04
Variability in % foliage cover 15-20m	-0.84**	-0.07
% foliage cover 20-25m	-0.80**	-0.05
% foliage cover 2-3m	-0.78**	0.04
Variability in % foliage cover 20-25m	-0.74**	-0.17
Variability in tree height	-0.71**	-0.02
Variability in % foliage cover 5-10m	-0.68**	-0.01
Shrub density (stems/ha)	-0.68**	0.05
% foliage cover 25-30m	-0.66**	-0.07
% foliage cover 0.5-1m	-0.60**	-0.01
Variability in tree density	-0.58**	0.11
Variability in % foliage cover 25-30m	-0.58**	-0.21*
% foliage cover 1.5-2m	-0.53**	0.05
Variability in tree DBH	-0.52**	0.09
% foliage cover 1-1.5m	-0.51**	0.05
% foliage cover > 30m	-0.45**	-0.03
Variability in % foliage cover 1.5-2m	-0.43**	0.03
Variability in % foliage cover > 30m	-0.36*	-0.16
% foliage cover 0-0.5m	-0.33*	-0.17
Variability in % foliage cover 1-1.5m	-0.25*	-0.02
Variability in % foliage cover 2-3m	-0.22*	0.09
Variability in shrub density	-0.17	0.06
% foliage cover 3-5m	-0.08	0.02
Average DBH (cm)	-0.03	-0.07
Variability in % foliage cover 0.5-1m	0.02	-0.09
% foliage cover 10-15m	0.1	-0.17
Variability in % foliage cover 3-5m	0.12	0.04
% foliage cover 5-10m	0.15	0.05
Variability in % foliage cover 0-0.5m	0.38**	0.24*

** significant at $P < 0.0001$ level

* significant at $P < 0.05$ level

4.8. Figures

Figure 4-1. Location of Mabira Forest and surrounding areas in southern Uganda. Solid gray indicates primary forest, vertical lines are secondary forest, and stippled areas are smallholder agriculture. Other land-uses (large-scale agriculture, bushland, etc.) are represented by white.

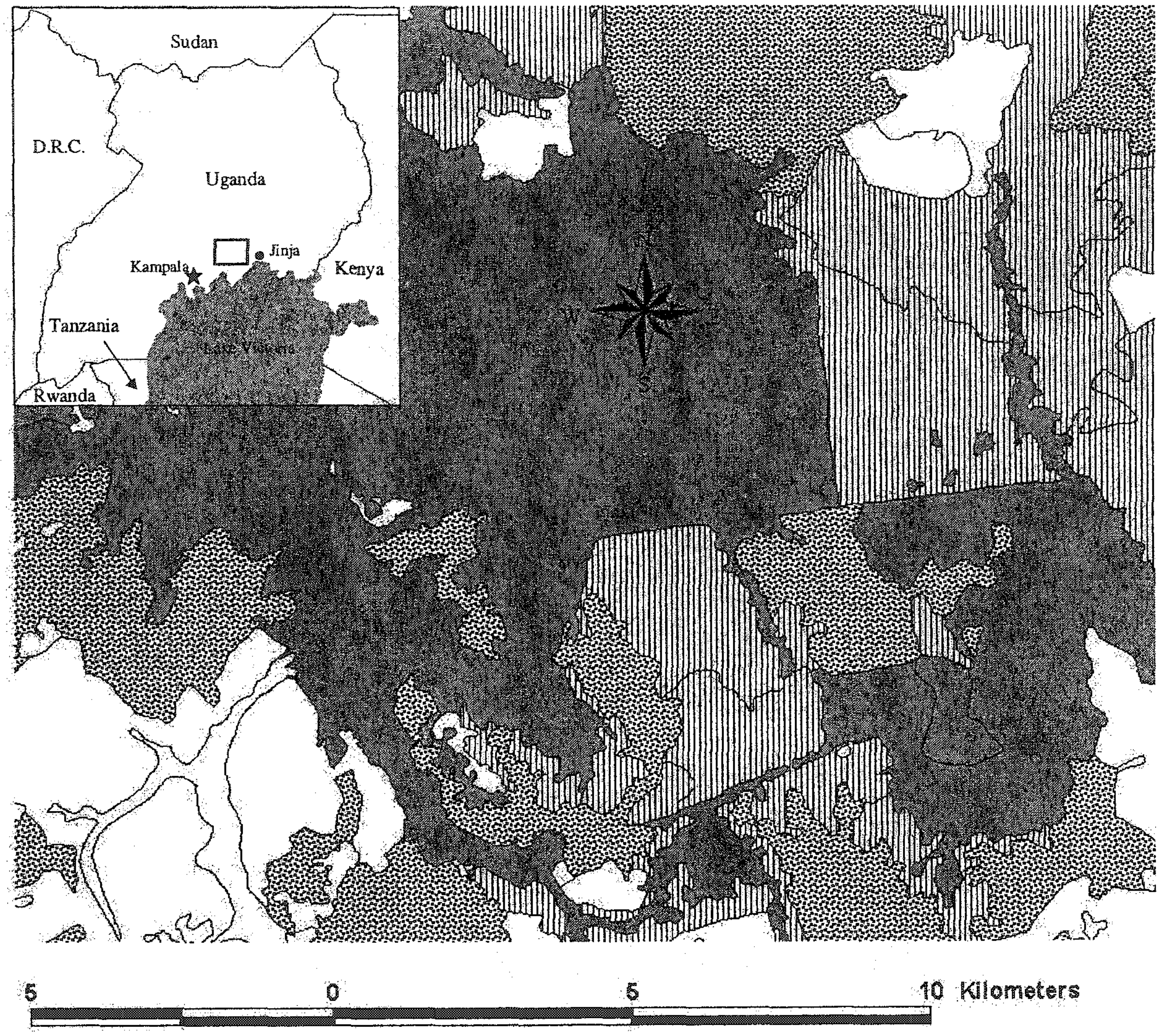


Figure 4-2. Vertical foliage profile for primary forest (filled diamonds), secondary forest (squares), and smallholder agriculture (triangles). Proportion intersected is calculated by dividing number of points that foliage intersects by the total number of points sampled (20 per station for each height interval). Points are plotted at the mid-range of the height interval assessed; see Methods for height intervals. The 30 m + interval is plotted at 32.5 m.

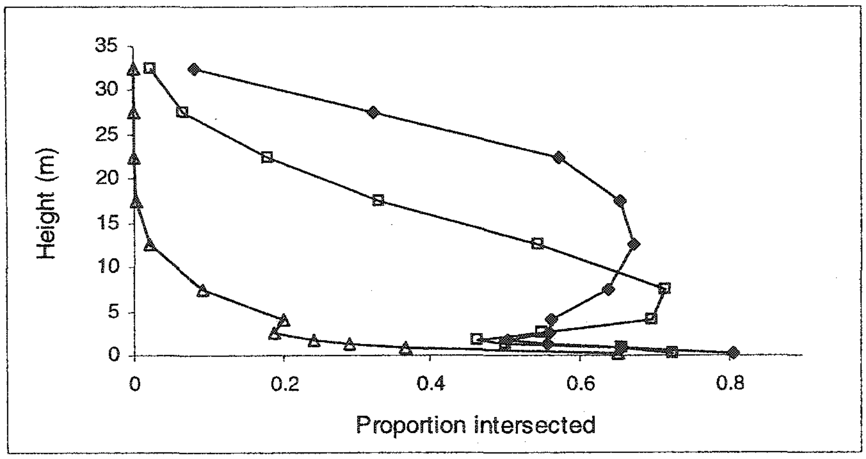


Figure 4-3. Scatterplot in station-space of Detrended Correspondence Analysis (DCA) axes 1 and 2. Each station is positioned at the centroid of the ordination scores of all species that occurred at that station. 95 % confidence ellipses are given for primary forest (filled diamonds), secondary forest (squares), and smallholder agriculture (triangles).

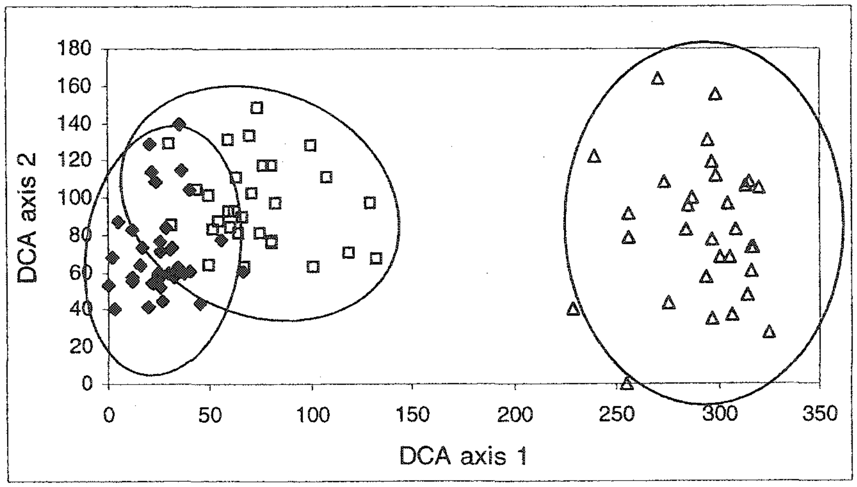


Figure 4-4. Scatterplot in species-space of Detrended Correspondence Analysis (DCA) axes 1 and 2. Each species is positioned at the centroid of the ordination scores of the stations at which it was found. Guilds represented are forest specialists (filled diamonds), forest generalists (squares), forest visitors (triangles), and open habitat specialists (x's).

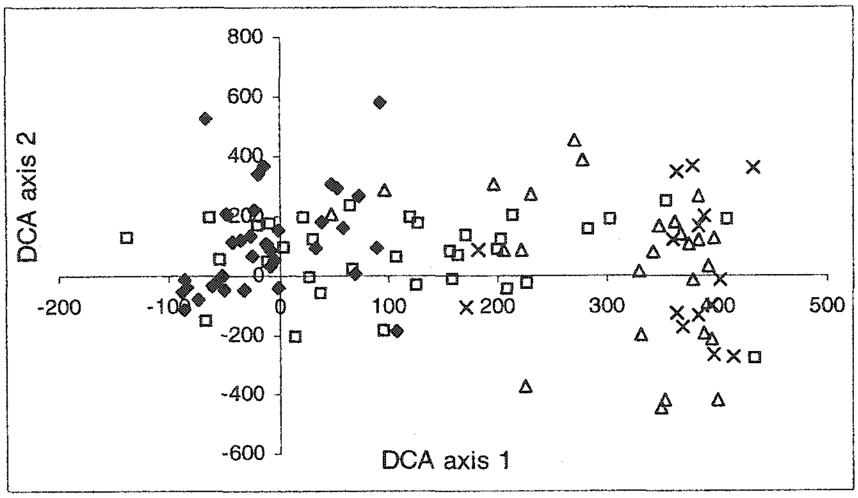
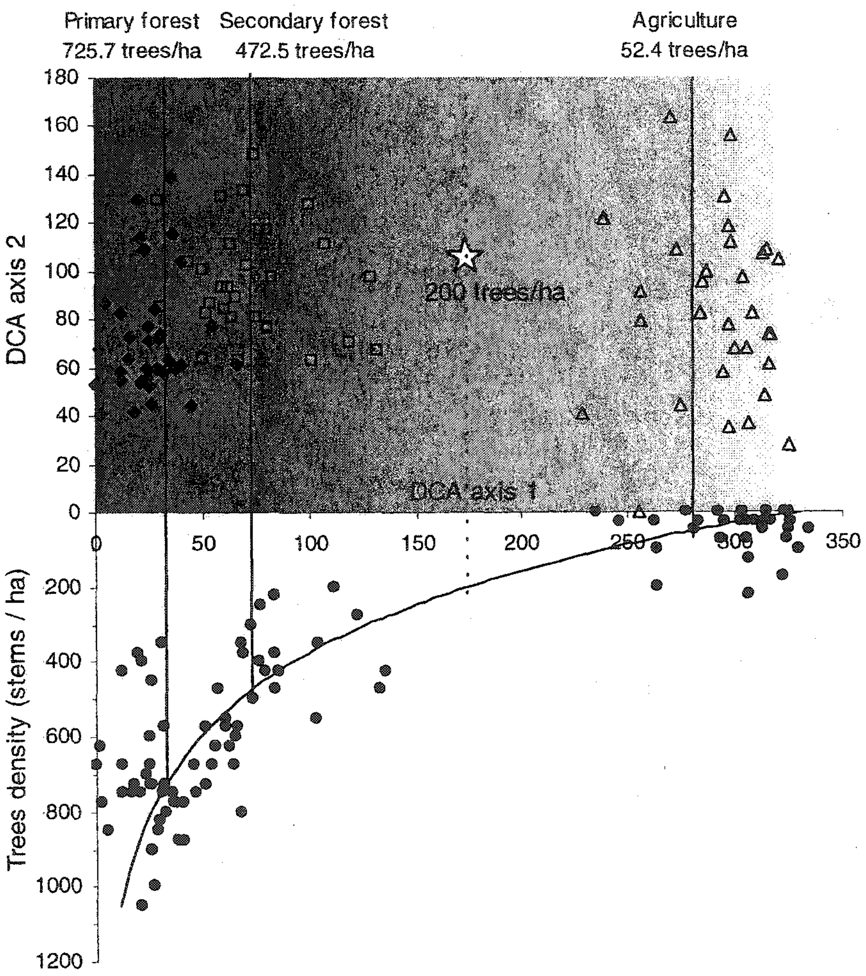


Figure 4-5. Schematic representing the relationship between tree density and community structure. *Upper panel.* - Scatterplot of DCA axes 1 and 2 in station space. Shading represents gradient from forest specialist community (dark) to open habitat community (light). Drop lines from lower panel show mean tree densities for primary forest (filled diamonds), secondary forest (squares), and agriculture (triangles). Dashed drop line and star indicate the DCA axis 1 value corresponding to a tree density of 200 trees/ha. *Lower panel.* - Relationship between tree density and first axis of DCA. Line for the best fitting equation (DCA1 = 321.2 * EXP (0.003 * Tree density) is shown.



5. Tourism and the value of biodiversity at Mabira Forest, Uganda[‡]

5.1. Introduction

Integrated conservation and development projects (ICDP), which combine local environmentally-based industries with the maintenance of biodiversity as dual conservation/development goals, are a standard sustainable development approach in many developing countries (Salafsky et al. 2001, Salafsky and Margoluis 1999). It is often assumed that ICDP's will result in the conservation of the natural resource(s) in question, while at the same time leading to increased benefits for local communities who may have forgone less environmentally-friendly development strategies (Salafsky and Wollenberg 2000, Infield and Adams 1999). Nature-based tourism[1] is a key component of ICDP's in many developing countries (Salafsky et al. 2001, Isaacs 2000, Bookbinder et al. 1998). Because nature-based tourism is a non-consumptive activity that should rely on intact natural resources to generate revenue, it is regularly viewed as a "win-win" situation for conservation and sustainable development.

Quantitative assessments of ICDP's are rare, and those that exist have shown mixed results in terms of both environmental and economic goals (Balmford et al. 2002, Barnes et al. 2002, Salafsky et al. 2001). More particularly, assumptions regarding nature-based tourism, the conservation of biodiversity, and community welfare are not supported by empirical research. There is little evidence to suggest that tourists are interested in biodiversity *per se*, rather than spectacular landscapes, attractive lodging facilities, or a few charismatic species, when visiting a protected area. Tourists have various reasons for visiting tropical protected areas, and hence relying on nature-based

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[‡] A version of this chapter has been submitted for publication. Naidoo, R., and W.L. Adamowicz. 2003. Biodiversity and nature-based tourism: the potential for sustainable development in Uganda. *Environment and Development Economics*, in review.

[1] I use this term rather than the more restrictive "ecotourism" for several reasons. Nature-based tourism can be more flexibly defined as any type of tourism that has as its primary purpose the viewing and/or enjoyment of nature, including hiking, birdwatching, safaris, etc. While the term ecotourism implies ecologically-friendly tourism, such is not always the case (Obua, 1997; Isaacs, 2000), and confusion exists as to its exact meaning.

tourism to conserve biodiversity may be risky if tourists are not particularly concerned about biodiversity.

To predict whether nature-based tourism can lead to protection of biodiversity and increased welfare of local residents, we must investigate the relative preferences of tourists in the context of protected area visitation. Such an investigation should also include a means of quantifying how tourists value various levels/states of biodiversity. If nature-based tourism is to effectively conserve biodiversity, tourists' behaviour must lead to elevated revenues for areas rich in biodiversity. Assuming appropriate transfer mechanisms to those who control the fate of an area's natural resources, this would then provide an incentive to maintain natural ecosystems with high levels of biodiversity in protected areas.

Measuring values for biodiversity is a difficult proposition. The majority of attempts have involved willingness-to-pay approaches, because of the non-market nature of biodiversity conservation (Kosz 1996, Loomis and White 1996, Adger et al. 1995, Moran 1994; but see Montgomery et al. 1999). But these passive-use values are seldom ones that can be captured by local communities. Passive-use values often refer to circumstances that are global or regional in nature (Adger et al. 1995), and in many instances are values for phenomena that have no obvious and direct connections to real-world tradeoffs or economies (Gowdy 1997). Therefore while passive-use values can provide a rough indication of magnitude of preference for certain situations, they may not be useful for policy-making at local levels unless international mechanisms to capture them can be developed (Pearce 1996).

In the case of nature-based tourism, a market for biodiversity may exist among nature tourists, and hence this is a direct-use value that in theory may be useful in assessing sustainable development options. Two issues surrounding its application are: i) how can one accurately measure the values tourists place on biodiversity?; and ii) what mechanisms can be used to ensure that local communities capture this value? Here I deal primarily with the first issue. As several papers have pointed out, many ICDP's are failing because revenue flows from "local" industries are not reaching the community members originally targeted (Salafsky et al. 2001, Murombedzi 1999, Infield and Adams 1999, Bookbinder et al. 1998). People living near the conservation area therefore prefer to have guaranteed but unsustainable access to the resource, rather than foregoing resource exploitation for compensation that may never arrive. Although this is obviously a critical issue for ICDP's, it is beyond the scope of this study.

I focus here on the demand for nature-based tourism, as a function of biodiversity, that could benefit communities through the collection of entrance fees. The existence of a potential market for biodiversity among tourists means that a revealed preference approach to measuring the value tourists hold for biodiversity could be suitable. However, the logistics of such an approach would be extremely challenging, due to the large number of associated factors that would need to be accounted for, the large number of protected areas from which data would need to be collected, and the difficulty in deciding on which aspect of biodiversity would be quantified. For these reasons, a stated choice approach to the valuation of biodiversity is preferable.

Stated preference techniques involve asking respondents about their economic behaviour, given a well-described artificial market scenario. Stated preference techniques avoid some of the difficulties associated with revealed preference studies: they can assess demand for products which have no well-developed markets, they avoid issues of collinearity and low variability in explanatory variables, they are less demanding of research resources, and they can be experimentally designed to provide clear and easily-interpretable results (Louviere et al. 2000). Stated preference techniques have been used in a wide variety of applications (e.g., Bhat 2000, Revelt and Train 1998), and are particularly useful in environmental economics (Adamowicz et al. 1998, Adamowicz et al. 1994), where markets for ecological goods and services typically are non-existent, although these may nonetheless be highly valued by consumers.

This study employs a choice experiment approach to assess the potential for biodiversity to contribute to local community welfare via increased revenue from elevated visitation rates by nature tourists. A choice experiment is a technique that combines elements of experimental design, survey questionnaires, and discrete choice modelling to produce estimates of demand as a function of attributes of the goods and alternatives. Choice experiments are enjoying increased use in the field of environmental economics (Rolfe et al. 2000, Boxall and Macnab 2000, Blamey et al. 1999), and have been used in a tourism - tropical country context (Hearne and Salinas 2002). A comparison of the performance of choice experiments with actual consumer behaviour concluded that they provide accurate results (Carlsson and Martinsson 2001). Calibration of choice models with actual data can minimize hypothetical bias problems (Louviere et al. 2000).

The study was conducted in Uganda, an east African country high in biodiversity, politically stable enough to support a small but growing nature-based tourism industry, and in urgent need of sustainable development options for its impoverished population. I focussed on a forest reserve in the south of the country, and presented tourists and foreign residents with a choice experiment designed to elucidate their preferences for biodiversity relative to other attributes that may be important to them. I asked respondents to choose either the forest reserve of interest, or two possible substitutes, to visit on their next trip. The choice was based on entrance fee, travel time, lodging facilities, tour packages, landscape features, and biodiversity of each destination. I quantified preferences for all of these attributes, and assessed whether elevated levels of biodiversity have the potential to contribute to the welfare of communities living near the forest reserve.

5.2. Methods

Choice experiment modelling

Random utility theory, in which consumers make discrete choices from a set of alternatives, underpins the choice experiment approach. In random utility theory, the consumer is said to obtain utility U (conditional on their choice) from an alternative i by the following:

$$U_i = v_i + \varepsilon_i \qquad (1)$$

This conditional indirect utility function is composed of the systematic indirect utility component (v_i), and a random error component (ε_i). An alternative i will be chosen if it has a greater utility than alternative j. The probability of choosing i over j is thus

$$p(i) = \text{probability } (v_i + \varepsilon_i >= v_j + \varepsilon_j), \quad (2)$$

where i and j are elements of the choice set.

Assuming that the errors are type-I extreme value distributed, the probability of choosing i becomes

$$p(i) = e^{v_i} / \sum_j e^{v_j} \quad (3)$$

The standard multinomial choice model applies to choice experiments when v_i is defined as

$$v_i = \sum_j \beta_k X_i^k \quad (4)$$

where B_k is the coefficient on attribute X^k.

This model can be estimated by Maximum Likelihood techniques, and is a useful first cut at modelling choice behaviour. However, several well-known limitations apply. The most severe of these is the independence of irrelevant alternatives (IIA) property, which states that a change in the attributes of one alternative changes the probabilities of the other alternatives in proportion. This substitution pattern may not be realistic in all settings. Secondly, the coefficients of all attributes are assumed to be the same for all respondents in a choice experiment, whereas in reality there may be substantial variability in how people respond to attributes. Finally, the standard multinomial choice model assumes that unobserved factors are independent over choices, whereas one might actually expect such factors to be correlated within decision-makers (Train 2003).

To overcome such limitations, I estimated a random parameters logit model (RPL) using panel data (Hensher and Greene 2002). This specification assumes that an individual's utility i for an alternative k is described by

$$U_{ik} = X_{ik}\bar{\beta} + X_{ik}\tilde{\beta} + \varepsilon_{ik} \quad (5)$$

that is, that each person's utility deviates from the population mean $\bar{\beta}$ by the vector $\tilde{\beta}$. Correlation between repeated choices is thus obtained within individuals, which is realistic in a choice experiment setting, as long as there are no learning or fatigue effects while completing the survey, and if completing the survey itself leads to no changes in tastes. Unlike the standard MNL model, estimating the coefficients on X now requires estimating the distribution (form specified by the analyst) from which these B's arise. Readers interested in the mathematical details of RPL models should consult Revelt *et al.* (1998), Train (1998), Layton *et al.* (2000), and Train (2003).

Although this RPL model allows the analyst to assess the effects of unobserved heterogeneity, heterogeneity that might be explained by observable socioeconomic variables is not accounted for. Previous studies have interacted individual-invariant variables with choice experiment attributes to address this issue (e.g., Revelt and Train 1998). A more elegant way to address this within the RPL framework is to introduce heterogeneity among respondents in the mean of the parameter variable through individual variables such as age and income[2]. In other words, the specified parameter distributions are "shifted" by individual-level variables, and the significance of these shifts can be tested in a manner analogous to tests for typical attribute coefficients (Hensher and Greene 2002).

Design of the choice experiment

The description of each choice in terms of attributes, and the selection of choice alternatives (the "choice set") are critical to the design of a successful choice experiment (Louviere et al. 2000). Attributes must describe each alternative in realistic and thorough terms, such that the respondent can clearly differentiate between alternatives based on them. However, the number of attributes should not be so high as to ask the respondent

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[2] Another way to account for respondent heterogeneity is through a market segmentation approach (Louviere *et al.*, 2000). In my preliminary analyses I tested many different such approaches, including segments based on country of residence (expatriate residents of Uganda vs. tourists), purpose of trip visit (business, holiday, or visiting friends and relatives), and gender (male vs. female). While some slight differences in attribute coefficients were found, the overall similarity between models was great enough to warrant using aggregate models for analysis and policy simulations, and hence I present only these aggregate models in the paper.

to assimilate more information than s/he is capable of. The alternatives presented in the choice set must also be a realistic set of close substitutes that the respondent would consider if s/he were actually making a choice.

In this study, respondents were asked to choose from 3 protected areas that they could visit, assuming a trip origin at Kampala, the capital city of Uganda. Mabira Forest Reserve is a 300 km^2 patch of protected forest in the south of the country. Budongo Forest Reserve is a 825 km^2 protected forest in central Uganda, and Kibale National Park is a forest of 528 km^2 in western Uganda. All three protected areas are composed mostly of tropical lowland forest, and are well-known for their diversity of forest birds. In addition to the choice of these three protected forests, respondents were also allowed a choice of not visiting any of these forests.

I focus on Mabira Forest Reserve, and the preferences of nature tourists for attributes at this forest, because of related work on avian (bird) biodiversity that one of us has conducted there (Naidoo 2002). Birds are an appropriate taxonomic group to use in the context of tourist preferences for biodiversity. Birds are conspicuous, many different species can be easily identified by amateur naturalists or birdwatchers, and international birdwatching tours are increasing in popularity (Blondel 2000). In addition, birds are a good surrogate for overall biodiversity levels in Ugandan forests (Howard et al. 1998), hence high levels of avian biodiversity are indicative of biodiversity-rich areas across many taxonomic groups.

Because of its proximity to the capital Kampala, and to the country's second city Jinja, Mabira Forest Reserve exists in a zone of high human population density. The local residents are mostly smallholder farmers, with farms containing a mix of cash and subsistence crops, such as coffee, bananas, maize, cassava, ground nuts, and sweet potatoes, as well as scattered trees (Oduol and Aluma 1990). Living standards in the region are low, with a life expectancy of 47 years and annual household incomes of around 200$ U.S.[3] (Mrema et al. 2001, National Environment Management Authority 1997). Although it is officially prohibited to reside, graze livestock, or cultivate land in

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[3] All monetary values are expressed in 2001 U.S. dollars, unless otherwise noted.

the Reserve, funding for monitoring and enforcement is lacking, and violations are widespread (Howard et al. 2000), personal observation). Locals use the forest as a source of fuelwood, poles, construction material, wild fruit and vegetables, honey, fodder, and wild game (Mupada 1997), and agricultural encroachment within the Reserve boundaries is an issue of prime management concern. Determining whether economic incentives to halt forest degradation result from optimal management of the Reserve is thus a key question for managers of the forest.

The attributes that defined each choice were the following: travel time from trip origin (hours), entrance fee (U.S. $), number of bird species likely to be seen, whether the visit was part of an organized tour, what type of lodging facilities were available on-site, what type of landscape features the forest contained, and the likelihood of seeing large game animals. The attributes and their levels in the choice experiment are shown in Table 5-1. Because of experimental design constraints, I fixed the attributes of Kibale Forest National Park at their current levels[4], and varied only those of Mabira Forest Reserve and Budongo Forest Reserve. Attributes and their levels were based on reviews of the literature, personal observations, communications with relevant authorities, and potential policy implications of the results.

Given that there are two alternatives with 6 attributes each (4 of which have 4 levels and 2 of which have 2 levels) a total of (4^4 x 2^2) x (4^4 x 2^2) combinations of attribute levels are possible in a fully-factorial design. I reduced the number of combinations by using a fractional factorial design (Louviere et al. 2000) that considers only main effects and ignores potential interactions among attributes. The minimum number of profiles (attribute level combinations) necessary to estimate orthogonal main effects was 32. I divided these 32 profiles into two blocks of 16, and presented one block of 16 scenarios to respondents by means of a survey.

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[4] In some cases these entailed best-guesses or approximations. For example, I set number of bird species likely to be seen at Kibale at 40, as this seems to be a reasonable estimate for a tourist to expect on a day outing with no special effort made to detect bird species. Kibale also does not possess a luxury lodge, but does have a luxury tented camp, a much more comfortable level of accommodation than the other two parks in the choice set.

The survey consisted of an explanation of why the research was being conducted, the choice experiment section (Figure 5-1), a section on demographics, and an appendix which included a glossary of terms and photographs of landscape levels described in the choice experiment. Each respondent was required to complete the choice experiment section by selecting one of the four available options (visiting either Mabira, Budongo, Kibale, or none of them) in each of the 16 scenarios, based on the values of the attributes described above that varied for each scenario. Prior to the start of surveying, I pretested surveys to ensure that the instrument was clear and unconfusing to respondents. Questioning of park and tourism officials in Uganda regarding choice sets and attributes lent further confidence to my belief that the choice experiment was a realistic, artificial market setting.

The survey was administered in the departure lounge at the country's international airport in Entebbe by two Ugandan assistants, during July and August, 2001. Close to one thousand surveys were handed out to travellers waiting in the departure lounge. Of these, 132 were not filled in, representing a 13% refusal rate. In all, 861 surveys were collected with usable responses, representing a large sample of the potential tourists for Mabira Forest Reserve. 96.6 % of all surveys were either from tourists (80.1%) or from foreign residents of Uganda (16.5%). Since these two groups are the most relevant for policy purposes, I restricted the analysis to them.

Model estimation

Effects of continuous attributes (travel time, entrance fee, and bird species) were estimated by the mean and standard deviation of a normal distribution. I allowed for non-linearity in the specification by using the natural logarithm of birds and travel time.[5] For categorical attributes, effects-coded variables were used (Louviere et al. 2000). This method is similar to dummy variables, except that a categorical variable with *n* levels is replaced by *n*-1 effects-coded variables. The omitted level is referred to as the base case,

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[5] This specification seems logical, as using the natural logarithm of both birds and travel time assumes positive but diminishing utility to travellers as these variables increase towards some asymptote.

and the significance of coefficients on the other levels are relative to the base case (i.e., a significant positive coefficient indicates that this attribute level confers significantly greater utility than the base level). Selection of the base cases was arbitrary; these are indicated in Table 5-1.

Policy assessments

I was interested in determining whether elevated levels of biodiversity lead to increased tourist visitation, and hence whether they have the potential to increase community welfare. Other studies have shown that tourists are often willing to pay higher entrance fees than they currently do (e.g., (Schultz et al. 1998), but these studies have not asked whether biodiversity may be directly implicated as a cause. Considering entrance fee and bird species seen, I asked what an optimal management scheme for Mabira Forest Reserve would entail, with optimality defined as the maximization of revenue accruing to the park ecotourism centre. To construct such a scheme, I first calibrated the models to actual tourist data for the three reserves in the choice set[6]. Using the parameters estimated for the normal distributions of the random variables, I made 5,000 draws and calculated the average coefficients from these runs. These were then used to calculate alternative-specific constants that equalized model-predicted and actual proportions of visitors to each site, using attribute values that reflected current conditions at each site

Once these alternative-specific constants were estimated, the entrance fee at Mabira Forest Reserve was varied from 0 to 65$ in increments of 0.5$, and the proportion of visitors predicted to visit Mabira Forest was recorded. To incorporate stochasticity arising from the random variables, I made 1,000 draws from the parameterized normal distributions and found the entrance fee at which revenue was maximized. I repeated this procedure 100 times. This protocol was followed for each of

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[6] Data on visitors to Mabira Forest Reserve and Budongo Forest Reserve were supplied by the Uganda Forest Department, and data on visitors to Kibale National Park were supplied by the Uganda Wildlife Authority.

20, 40, 60, and 80 bird species likely to be seen at Mabira Forest. Finally, the proportion of visitors was converted to revenue in U.S.$ by multiplying the average number of visitors per year to these three parks by the proportion of visitors predicted to visit Mabira Forest Reserve, multiplied again by the value of the entrance fee paid, for each of the above scenarios.[7]

5.3. Results

Column one of Table 5-2 shows results from the standard multinomial model of tourist visitation. All coefficients are significantly different from zero, except for those on the primary forest variable and the tour variable. Respondents received negative utility from increased price, travel time, secondary forest (as compared to both forest types and agricultural areas), and tents (as compared to no lodging at all). Positive utility was conferred by increased numbers of bird species seen, cabins and luxury lodges (as compared to no lodging at all), both primary and secondary forest present (as compared to both forest types and agricultural areas), and a good chance of seeing large wildlife. This model correctly classified 47.6 % of choice experiment responses, and had a pseudo-rsquared[8] of 0.04 %.

Results from the RPL model are shown in column two of Table 5-2. For the effects-coded variables, the direction and significance of coefficients are the same as in the standard multinomial model, except that tour now confers significant negative utility

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[7] The number of tourist and foreign resident visitors was summed over each park from 1996-2001, and averaged over the 5-year time period to produce an annual value. This worked out to an annual average of 3,765 tourist and foreign resident visitors to the three parks. Actual number of visitors from 1996-2001 were: Mabira, 6224; Budongo: 4257; Kibale: 8343. Note that my policy simulations assume no growth in the overall tourist market of these three parks, whereas in reality the World Tourism Organization expects the tourism industry in Africa to quadruple by 2020.

[8] Pseudo-rsquares are the likelihood ratio index subtracted from unity, where the likelihood ratio index is the maximized log-likelihood function divided by the log-likelihood function when attribute coefficients are zero. They are a measure of goodness of model fit, with ratios of between 0.2 – 0.4 equivalent in magnitude to least-squares regression R^2's of 0.7 - 0.9 (Louviere *et al.*, 2000).

on average respondents, and the coefficient on tents is no longer significant. Coefficients on the birds and entrance fee continue to be highly significant, while the coefficient on travel time is no longer significant. In addition, standard deviations of the coefficients on continuous variables were all significantly positive. This indicates that there is considerable heterogeneity among respondents, in terms of their responses to these variables, that the standard multinomial model did not capture. Most notably, the RPL model provides a much better fit to the data, as reflected in the higher pseudo R-squared value (0.38).

Heterogeneity among respondents may be due to variation in tastes or other unobservable variables, or to variation in socioeconomic condition, which is observable to some extent. The RPL model of Table 5-2 addresses the first of these heterogeneity types, but not the second. To tease these two sources apart, age and income (as classes) of respondents were entered into the RPL model by constraining the distribution means of the continuous variables[9]. The results from this model are shown in column 3 of Table 5-2. No practical differences in the coefficients on birds and entrance fee were noted, and the results for all effects-coded variables were also similar. The coefficient on travel time is now positive, however, indicating that the mean response to increased travelling time is to increase utility, a finding at odds with most recreational choice studies. However, the standard deviation on travel time is much larger than those on birds and fee, indicating enormous variability in how travellers respond to this variable. Even so, the standard deviations of coefficients on birds and fee were again highly significant, indicating that age and income effects of respondents did not account for a large amount of the heterogeneity in responses, even though significant shifts in parameter distributions were observed for all combinations except travel time and age. The fit of this model also did not improve on that of the RPL model with no interactions (a pseudo R-squared value of 0.38).

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[9] Income is a standard variable used to explain individual-level variation in choice experiment studies (e.g., Revelt *et al.*, 1998). I included a respondent's age because I hypothesized that younger travellers ("backpackers") and older adults may differ in terms of their eagerness to make long trips, their willingness to pay higher entrance fees, and their interest in birdwatching.

Because interacting age and income with the continuous variables did not significantly improve model fit, I used the RPL model in Table 5-2 for all policy simulations. The share of visitors predicted to visit Mabira Forest was very close to the actual share (36% vs. 33%); this is another indication of the reliability of the model. Predicted shares for Budongo (29% vs 23%) and Kibale (35% vs. 44%) were slightly less accurate but nevertheless quite close to the true values. To calibrate the model predictions to these actual values, I added alternative-specific constants to each site to equalize actual and predicted visitation shares (constants added were Mabira: -0.09; Budongo: -0.235; Kibale: 0.22).

Revenue flows from these calibrated models for various levels of entrance fee and birds species seen are shown in Figure 5-2. Revenue accruing to the park ecotourism centre was maximized at an average entrance fee of 47.53$ (SD=2.28; range 37.5 – 62); a fee of this size resulted in average revenue flows of 29,919$ (SD=3,386; range 12,198 – 52,158). The number of bird species seen was a strong determinant of revenue flows. When tourists expected to see 20 bird species, revenue flows at the maximum entrance fee were 18,032$ (SD=2,346; range 12,198 - 25,196). When the number of bird species likely to be seen was 80, maximum revenue flows were 40,423$ (SD=4,287; range 27,662 – 52,158), for an average difference of 22,391$, or 7.4 cents per bird species per tourist. Note that these figures assume no additional collection costs for elevated entrance fees.

5.4. Discussion

General results

The choice behaviour of tourists and expatriate residents of Uganda was assessed in the context of visitations to protected areas using a choice experiment approach. Three different models were used to predict respondents' choices: the standard multinomial model (MNL), the random parameters logit model (RPL), and the RPL model with demographic variables.

Almost all of the attributes in the study contributed significantly to tourist choices of which park to visit. Respondents therefore appeared to be trading off parks by their attribute bundles, and not simply by one dominant attribute or by park name. Strong effects of bird species (positive), chance of seeing large wildlife (positive), entrance fee (negative), cabin (positive), luxury lodge (positive), secondary forest (negative), and both forest types (positive) were noted in all three models. Travel time, tour, tents, and primary forest were less consistent explanators of tourist choice.

The RPL model greatly outperformed the MNL model, indicating significant unobserved heterogeneity in responses to numbers of bird species seen, travel time, and entrance fee. The use of RPL models in consumer choice studies is increasing (Train 2003, Hensher and Greene 2002, Bhat 2000, Layton and Brown 2000, Revelt and Train 1998, Train 1998), and the results presented here argue strongly for its superiority over the conventional MNL. This is particularly so in view of the fact that the inclusion of demographic variables that constrain parameter distributions in the RPL model did not significantly reduce unobserved heterogeneity, and hence did not lead to a better model fit. Conventional techniques that attempt to account for heterogeneity by interacting demographic variables with model attributes (e.g., Boxall and Macnab 2000) may therefore still be leaving a great deal of heterogeneity unaccounted for.

As in many previous studies, "price" (in this case, entrance fee) entered negatively into respondents' utility functions. Given that the sample pool was those travellers already in Uganda, and hence their expenditures would already be orders of magnitude higher than the entrance fee range in the experiment[10], this result is reassuring in that respondents viewed park entrance fees as an important attribute. It has been suggested that park entrance fees are a very minor component of foreign tourists' expenses in developing countries, and hence that large increases in entrance fees may do little to dissuade tourists from visiting protected areas (Menkhaus and Lober 1996, Maille and Mendelsohn 1993). The results indicate that tourists are acting as price-sensitive

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[10] This would not necessarily be true for expatriate residents, however as mentioned previously, market segmentation models for tourists vs. expats showed no significant differences in responses to this attribute (or others).

consumers in the context of park visitation in Uganda, but that they are not very responsive to price changes[11]. The results from this study indicate that revenue could be maximized by increasing entrance fees at Mabira Forest Reserve, from their current 2.75 / 3.50$ (foreign residents / tourists) to 47$. This greater than tenfold increase in fees is in-line with empirical studies of nature-based tourism that estimate large consumer surpluses or WTP on the order of 8-30 times greater than park entrance fees (Barnes et al. 1999, Schultz et al. 1998, Menkhaus and Lober 1996, Moran 1994, Maille and Mendelsohn 1993). Interestingly, one study that found actual entrance fees and tourists' WTP to be similar was that of Chase et al. (1998), which was conducted shortly after Costa Rica raised entrance fees in its parks tenfold. It seems clear that in general, entrance fees for foreign tourists in developing countries could be raised significantly in order to generate increased park revenues. It is equally clear, however, that a host of political factors may make such large increases in entrance fees difficult or undesirable to implement (Chase et al. 1998).

Biodiversity – ecotourism

The number of bird species likely to be seen was a strong positive predictor of choosing a particular park to visit. Because I specified the natural logarithm of birds seen, diminishing returns were observed as the number of species increased. These results provide evidence that biodiversity *per se*, i.e., the number of different species in a given situation, contributes to nature-based tourism by enhancing the attractiveness of a protected area to tourists. This study therefore upholds one of the most cited (yet poorly quantified) benefits of ecotourism: that biodiversity is a main reason why tourists visit protected areas, and hence the maintenance of critical biodiversity habitat can provide economic returns. These results are also at odds with a number of recent studies which describe the relationship between ecotourism and conservation of biodiversity as ambiguous at best, or inimical at worst (Isaacs 2000, Bookbinder et al. 1998).

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[11] The price elasticity of choice for Mabira Forest Reserve was a relatively low –0.303, indicating an inelastic demand (percent change in visitation probability less than the percent change in price).

At least for forested parks in Uganda, the positive relationship between probability of visitation and bird biodiversity is a compelling reason for management scenarios that maintain or enhance the possibility of large numbers of bird species being seen during a tourist's visit. The most obvious way to achieve this goal is to maintain sufficient habitat for large numbers of forest species to persist in protected areas. Bird species in forested areas in Uganda show a typical species-area relationship, with greater numbers of species found in larger areas[12]. Maintaining or increasing the areal extent of forest reserves will thus increase the number of bird species found in these reserves. More specifically, remaining tracts of old-growth forest should be conserved, as old forest stands in Mabira Forest Reserve contain as many or more species per unit area than the more common secondary forest, and bird communities are also quite different in old growth stands as compared to secondary forest (Naidoo 2002).

It should be noted that strictly speaking, the number of bird species likely to be seen on a trip to a protected area need not be positively correlated with bird biodiversity in that park. All three parks in the choice set of the experiment contain far greater numbers of bird species than the upper limit of the bird species attribute (the upper limit was 80 bird species seen, as compared to species lists of 287 for Mabira, 359 for Budongo, and 325 for Kibale). Factors such as the park's trail network, bird guiding services, specialized infrastructure (blinds, canopy tower, etc.), and vegetation density will therefore be very important factors influencing how many of these bird species are seen. The number of bird species seen on a trip will be uniquely correlated with bird biodiversity only when other factors such as those above are constant among parks. The magnitude of these impacts on bird species seen is an empirical question, however, and does not detract from the theoretical significance of bird species per unit area as a positive influence on the number of bird species seen.

Sustainable development

Forests are at the forefront of conservation efforts because of the seemingly large discrepancy between their standing economic value, and their value as a supply of timber

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[12] Log(bird species) = 0.48 * log(area) + 1.03; data from Howard et al.(2000).

and/or agricultural land. Because many valuable environmental services of standing forests are not traded in the market, a large number of valuation studies have attempted to quantify both market and non-market benefits of forests in both states (standing vs. logged). While some studies have shown that certain non-market environmental services from standing forests have rather large economic values (Kremen et al. 2000, Mendelsohn and Balick 1995, Adger et al. 1995), these values were generally regional or global in nature, and hence institutions to capture this value were either weak or non-existent. In general, for a forest with no official or *de facto* protected status to remain standing, its economic value as a standing forest must not only be higher than its value as timber or agricultural land, but this value must be captured by the relevant decision-making agents (Kremen et al. 2000).

Valuation of a forest in terms of its recreation value for nature-based tourism is practical because this is a market-based value that can in theory be captured by those agents involved in managing the forest: government and local residents. The standing-forest value I estimate for Mabira Forest is interesting because one attribute of the forest that was valued was biodiversity, a non-market commodity typically very difficult to measure. At current average tourism levels, I estimate that nature-based tourism in Mabira Forest Reserve generates approximately 7,000$ U.S. in revenue per year, or 0.23$/ha/yr[13]. The optimal pricing analysis suggests this is a serious undervaluation: raising the entrance fee to 47$ for tourists and foreign residents would result in revenues from 18,032$ (assuming 20 bird species seen) to 40,423$ (80 bird species seen) from entrance fees alone[14]. Average annual values per hectare of forest would thus rise to between 0.60 – 1.35$.

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[13] The exact figure is 6,983.34 $, assuming the average exchange rate (Interbank, April-September 2001) of 1,800 Ugandan Shillings for one U.S. dollar. Revenue data are from the Uganda Forest Department, and include revenue generated from entrance fees for Ugandan citizens (1,000 Ush for one-day entrance fee), foreign residents of Uganda (5,000 Ush), and foreign tourists (6,000 Ush), as well as camping and cabin fees.

[14] Ecotourism revenue at Mabira Forest from visits by Ugandan citizens is currently ~1,200$/yr; assuming prices and visitation rates for Ugandan citizens remain at current levels, adding this sum to the revenue

While comparisons of per-unit area measures of value can be misleading because of the importance of local economic and physical conditions, it is nonetheless interesting to compare the results to other such estimates from developing countries. Gossling (1999) reviewed per-hectare estimates for forest value based on entrance fees; values ranged from 0.15 to 3.6$/ha/yr for forest reserves in Costa Rica and Ecuador. Kremen et al. (2000) assessed the economic costs and benefits of an ICDP for a forest reserve in Madagascar; they found that the net present value (NPV) of the park managed for ecotourism was 19.1$/ha (U.S. 1996), whereas at the same discount rate and time horizon, I estimate NPV's of 11.98 - 26.95$ for Mabira Forest. More generally, my estimate of the standing value of Mabira Forest is similar to other recent estimates of tropical forests based on non-consumptive or sustainable management (Godoy et al. 2000, Kremen et al. 2000). These estimates of the standing value of tropical forests are significantly lower than extractive management schemes, and are also lower than earlier, more optimistic estimates (Peters et al. 1989). In part, this is because these later studies have calculated values that are capturable by those agents whose decision it is to conserve or convert the forest. While other indirect or passive values may hold extremely large values at the global level (e.g., Adger et al. 1995), such values remain in the theoretical realm only, unless institutional mechanisms for capture by the relevant agents exist.

I have demonstrated that regardless of entrance fee levels, it appears that increased amounts of revenue can be generated by allowing tourists the possibility of seeing greater numbers of bird species at Mabira Forest. Bearing in mind the caveats referred to earlier, the conservation of forest within the reserve will generally increase this possibility. Hence, maintaining bird biodiversity is economically beneficial to the Forest Department, which runs the ecotourism centre. In theory, the communities surrounding the forest reserve may also benefit, as an agreement between community leaders and the Forest Department entitles them to some of the receipts from the ecotourism centre (Mupada 1997). Assuming an average household income of 200$,

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figures above results in total revenues of 17,609 – 31,661$. Corresponding per-hectare values are 0.59 – 1.06$.

mostly from agricultural products (Mrema et al. 2001) and a dependent population of 2,700 households (the approximate number of households in Najjembe sub-county, which is the administrative district currently covered by the agreement between local communities and the ecotourism centre), the local cash agricultural revenues are approximately 540,000$. Optimal revenue flows to the ecotourism centre are therefore 3.3 – 7.5 % of the total local economic output. Given that per-capita incomes are so low and that most households do not get enough hard cash from on-farm activities to meet their household needs (Mrema et al. 2001), redistribution of even a portion of the ecotourism revenue would significantly benefit local communities.

It is clear however, that ecotourism benefits, even at the revenue-maximising fee, would not generate windfall gains for the local community. Furthermore, mechanisms to implement revenue-sharing at Mabira Forest are weak, with revenue transfer operating in an *ad hoc* and confusing manner. Experience in other areas of Uganda with such community revenue-sharing schemes have met with mixed results, with unsteady institutional implementation a key weakness to programs which nevertheless have improved local attitudes towards adjacent protected areas (Archabald and Naughton-Treves 2001, Infield and Adams 1999). Assuming appropriate revenue-sharing mechanisms can be developed, a thorough economic analysis of villagers' incentives to degrade or conserve the forest would assess the economic value of using the forest in a destructive or non-sustainable way, and compare this to its value as a nature-based tourism site. I have presented such an analysis in the following chapter. Nevertheless, the analyses presented here show that biodiversity conservation does have modest potential to contribute economically to sustainable development.

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5.6. Tables

Table 5-1. Attributes and levels of the choice experiment.

Attributes	Levels
No. bird species seen	4 (20,40,60,80)
Entrance fee (US $)	4 (5,15,25,40)
Travel time (hours)	3 (1,5,6) **
Visit part of tour?	2 (yes, no *)
Lodging facilities	4 (none * tents cabin luxury lodge)
Landscape features	4 (Primary forest, secondary forest, agriculture * Primary forest Secondary forest Primary and secondary forest)
Chance of seeing large wildlife	2 (very slim chance *, very good chance)

* base case for effects coding

** alternative-fixed attribute

Table 5-2. Tourist visitation models derived from the choice experiment data (coefficients, with *t*-values in brackets).

Attribute	MNL	RPL	RPL w age/income
Attribute means			
ln (Birds)	0.19	0.66	0.79
	(16.2)	(24.4)	(11.1)
Entrance fee	-0.021	-0.025	-0.045
	(-17.0)	(-12.5)	(-9.0)
ln (Travel time)	-0.19	-0.047	0.43
	(-7.6)	(-0.6)	(2.6)
Part of tour	-0.0081	-0.073	-0.075
	(-0.5)	(-4.1)	(-4.3)
Tents	-0.079	-0.024	-0.0098
	(-2.8)	(-0.7)	(-0.3)
Cabin	0.25	0.37	0.36
	(9.4)	(11.4)	(10.6)
Luxury lodge	0.24	0.15	0.16
	(10.0)	(5.3)	(7.2)
Primary forest	-0.034	-0.018	-0.0031
	(-1.2)	(-0.6)	(-0.1)
Secondary forest	-0.16	-0.15	-0.16
	(-5.7)	(-4.5)	(-4.4)
Both forest types	0.18	0.077	0.089
	(7.9)	(2.8)	(3.3)
Chance of wildlife	0.56	0.68	0.68
	(33.8)	(35.0)	(52.3)
Attribute standard deviations			
ln (Birds)	-	0.77	0.72

		(26.7)	(34.9)
Entrance fee	-	0.040	0.040
		(19.9)	(20.9)
ln (Travel time)	-	2.36	2.39
		(24.1)	(38.9)
Heterogeneity in attribute means by age/income			
ln (Birds) - age	-	-	-0.065
			(-3.5)
ln (Birds) - income	-	-	0.017
			(2.3)
Entrance fee - age	-	-	0.0047
			(-3.1)
Entrance fee - income	-	-	0.0007
			(-1.1)
Travel time - age	-	-	-0.19
			(-4.3)
Travel time - income	-	-	0.023
			(1.3)
Log-likelihood	-16,516	-11,707	-9,983
Pseudo R^2	0.44	0.38	0.38
Number of observations	13,623	13,623	11,623

5.7. Figures

Figure 5-1. An example of one of the 16 choice scenarios presented to each respondent in the choice experiment portion of the survey.

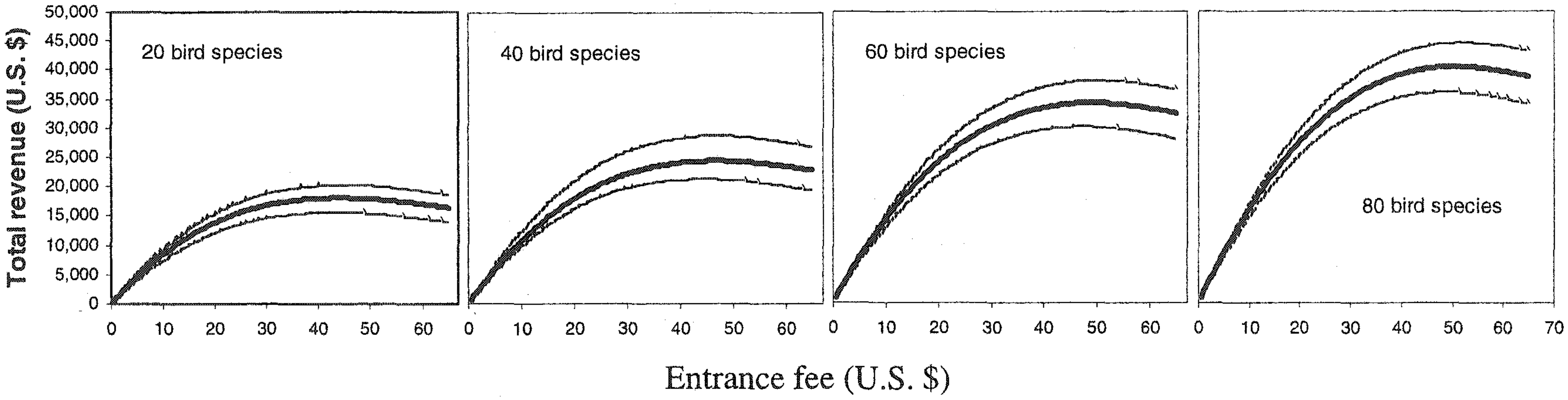
Assuming the following nature parks were the **ONLY THREE** choices available when you were making your decision for where to visit on your next trip out of Kampala, which one of them would you have picked?

Features of nature parks	**Mabira Forest Reserve**	**Budongo Forest Reserve**	**Kibale National Park**	**I WOULD NOT VISIT ANY OF THESE PROTECTED AREAS ON MY NEXT TRIP**
Travel time from Kampala	1 hour	5 hours	6 hours	
Entrance fee (U.S. $)	10	10	15	
Destination part of package or tour?	No	No	Yes	
Lodging facilities	Cabin	Tent	Luxury lodge	
Landscape features	Forest and smallholder agriculture	Primary and secondary forest	Primary and secondary forest	
Bird species you may see	60	40	60	
Chance of seeing large wildlife	Very slim chance	Very slim chance	Very good chance	

☐ ☑ ☐ ☐

Please Tick ONE Box Only

Figure 5-2. Revenue flows to the Mabira Forest ecotourism centre. Each curve (heavy lines) represents the change in revenue as entrance fee increases for a given level of bird species seen. Standard deviations above and below each curve are also shown (weak lines).



6. The potential for market-based biodiversity conservation at Mabira Forest, Uganda

6.1. Introduction

Concerns about the continuing degradation of natural ecosystems have stimulated various mitigative response strategies from scientists and policy-makers (Daily and Walker 2000, Pimm et al. 2001). In addition to the enormous contributions from the natural sciences, insights from economics have begun to affect thinking regarding conservation biology (Costanza et al. 1997, Kremen et al. 2000, Balmford et al. 2002). The proliferation of studies on the economic value of ecosystem goods and services, to name just one area of research, attests to the enthusiasm with which economic analysis is being applied to conservation problems (Godoy et al. 2000, Costanza et al. 1997, Peters et al. 1989). However, economic research on biodiversity, narrowly defined here as the variation in species numbers of a given taxonomic group within a defined geographical area, has lagged behind research on its ecological aspects. Two areas of conservation biology in which techniques from economics can make major contributions are the estimation of values held by society for biodiversity, and quantifying the costs of providing biodiversity at varying levels to a society in which resources are scarce and should be efficiently allocated.

The cost of supplying various levels of biodiversity has been researched in the context of conservation reserve design (Margules and Pressey 2000). Building on algorithms that predict the "best" network based on the spatial pattern of species distributions, several studies have recently asked how incorporating costs of supplying various reserve configurations affects provision of biodiversity (Ando et al. 1998, Montgomery et al. 1999, Polasky et al. 2001). These studies used the explicit or implicit market value of land to estimate the opportunity costs involved in setting aside protected areas, and showed that reserve design algorithms that include costs result in similar numbers of species protected ("supplied"), and lower expenditures than conservation programs that ignore supply costs.

A different approach was taken by Balmford and his colleagues, who used surveys of protected area managers to estimate the costs of establishing a global network of conservation reserves that protects 10-15% of natural regions (James et al. 1999), and then integrated these data with country-level mammalian biodiversity indices (Balmford et al. 2000). Their results also highlight the considerable cost-efficiency in supplying biodiversity that can be obtained by integrating cost data in conservation strategies. They also suggest that global conservation costs are relatively low, less than one-fifth the value of environmentally-damaging government subsidies. The costs of establishing a representative reserve network in the United States are also suspected of being low relative to other governmental expenses, such as road maintenance (Shafer et al. 2002).

Unfortunately, detailed studies that reveal relatively low supply costs are only one side of the coin in determining what "optimal" expenditures on conserving biodiversity should be. A fundamental economic theory holds that in a well-functioning market, it is the combination of both the supply *and* the demand curves that results in the price and supply of a good (Samuelson and Scott 1971). Hence, to rigorously determine optimal expenditures on conservation of biodiversity, it is necessary to understand the shape and scale of the demand for (or benefits of) biodiversity. I know of no studies that have provided an estimation of such a curve for biodiversity, although this lack of information has been identified as a research priority (Montgomery 2002).

As a first estimate of the potential for market based conservation biodiversity, I present an analysis of avian biodiversity at a rainforest reserve in Uganda. I focus on species richness of birds for several reasons. Birds are conspicuous and charismatic, many different species can be easily identified by amateur naturalists or birdwatchers, and international birdwatching tours are increasing in popularity (Blondel 2000). In addition, birds are a reasonable surrogate for overall biodiversity levels in Ugandan forests (Howard et al. 1998), hence high levels of avian biodiversity are indicative of biodiversity-rich areas across different taxonomic groups. I estimate the cost of various levels of biodiversity as the opportunity costs of conserving forest bird habitat, and convert this to bird species numbers using a species-area function for forests in Uganda. I estimate benefits of avian biodiversity by experimentally assessing tourist preferences for bird species numbers. From the resulting cost and benefit assessments I identify feasible states of biodiversity that could arise in a market-based setting, and discuss factors that could change these market outcomes. I conclude by discussing these results in the context of the recent literature on economic costs and benefits of biodiversity.

6.2. Methods

Study site

I conducted the study at Mabira Forest Reserve, a 300 km^2 patch composed of relatively intact tropical rainforest, regenerating secondary forest, and small-scale agricultural enclaves within the forest. This is the only large remaining forest of its type in southern Uganda, and contains moderate levels of biodiversity compared to other Ugandan forests: 199 butterfly species, 143 forest bird species, 97 moth species, and 312 tree species (Davenport et al. 1996). Because of its proximity to the capital Kampala, and to another large urban centre, Jinja, Mabira Forest Reserve exists in a zone of high human population density. The local residents are mostly smallholder farmers, with farms containing a mix of cash and subsistence crops, such as coffee, bananas, maize, cassava, ground nuts, and sweet potatoes, as well as scattered trees (Oduol and Aluma 1990). Living standards in the region are low, with a life expectancy of 47 years and an adult literacy rate of 60% (Mrema et al. 2001, National Environment Management Authority 1997).

Although it is officially prohibited to reside, graze livestock, or cultivate land in the Reserve, funding for monitoring and enforcement is lacking, and violations are widespread (Howard et al. 2000, personal observation). Locals use the forest as a source of fuelwood, poles, construction material, wild fruit and vegetables, honey, fodder, and wild game (Mupada 1997), and agricultural encroachment within the Reserve boundaries is an issue of management concern. As a forest reserve, some timber harvesting also occurs at Mabira Forest, along with illegal pitsawing, mainly for charcoal burners who supply the growing markets of Kampala and Jinja. Tensions between the forest department and locals have been high since 1988, when settlers who invaded the forest in the mid-1970's with the blessing of the Idi Amin government were ejected from within the boundaries.

In 1996, a donor-funded initiative established an ecotourism center at the forest, and since then small but growing numbers of tourists have visited the reserve (3842 in 2000). A portion of the proceeds from the ecotourism centre are distributed to surrounding communities in an ad-hoc manner, in the hope of increasing awareness of the potential economic benefits of preserving the forest. There is no set percentage of revenue allocated; community-proposed projects are evaluated intermittently by a committee composed of various stakeholders, and funding is granted based on available resources and community-level project benefits. No previous research has been conducted on economic incentives for forest conservation among local farmers, nor on the nature tourist market for Mabira Forest.

The research here focuses on potential conditions of a market involving "buyers" (nature tourists) and "sellers" (local residents) of avian biodiversity. While the forest department is a major stakeholder in the forest, lack of enforcement and corruption amongst forestry officials leave local stakeholders as a significant force behind land-use change in the region. Nevertheless, the continued existence of a large block of forest in this area of extremely high human population density is a testament to its protected area status. Given chronic funding shortages and a push in the tropics for conservation to "pay its way" (Langholz and Lassoie 2001), I examine management scenarios through which conservation of the forest is funded through tourist receipts. I also assume that it is possible to develop an effective mechanism for transferring tourism revenues from the ecotourism centre to the surrounding community, and that institutions can be developed such that economic benefits of preserving the forest accrue to local farmers and are considered by farmers when making land-use decisions.

Opportunity costs of biodiversity

I assume that the opportunity cost of biodiversity is equivalent to the opportunity cost of not converting forest habitats used by obligate forest bird species to agriculture, the dominant land-use in the area surrounding the forest. In the absence of spatially-referenced data on land prices for Mabira Forest Reserve, I modelled land values by integrating known returns to agriculture in the region with the spatial probability of deforestation. I assume that the economic rent R_i of an agricultural plot of land *i* is equivalent to the benefits derived from agriculture (P_iQ_i) minus the costs of production (C_iI_i). A plot of forest will therefore be converted to agricultural land when the benefits of doing so outweigh the costs:

$$R_i = P_iQ_i - C_iI_i \qquad (1)$$

$$A_i = 1 \text{ if } R_i > 0,\ A_i = 0 \text{ if } R_i \leq 0 \qquad (2)$$

where P are output prices, Q are quantity of outputs, C are input prices, and I are quantity of inputs, and $A_i = 1$ when a plot is converted to agriculture (deforested), and $A_i = 0$ when left as standing forest. As spatially referenced data for the above parameters are generally unavailable, I assume that Q is a function of biophysical variables that influence crop productivity, P and C are increasing functions of transportation costs, and population density affects P,C,Q, and I through the size of the labour pool, the size of output markets, and the demand for agricultural land (Chomitz and Gray 1996, Deininger and Minten 2002, Pfaff 1999).

More specifically, I assume that transportation costs are the prime determinant of agricultural input costs and output prices, and that as distance to market increases, input costs will increase and output prices will decrease, a consistent finding in the empirical literature (Minten and Kyle 1999). I include in the model distance estimates to the nearest paved road, road of any type, and village or town, as well as distance to two of the major urban markets in the area (Jinja and Lugazi). Increases in any of these variables are expected to increase input prices and lower output prices, and therefore deforestation is expected to decrease with increased transportation costs.

I included variables to control for the potential effects of differences in biophysical factors on crop productivity. The choice of these variables was limited to those expected by theory to affect crop growth and that were available for the study area. These included slope, elevation, soil type, distance from the nearest river, distance to the nearest agricultural plot, and distance from the geographical center of the forest. Sites close to a river have a greater chance of flooding than those further away; since permanent cultivation is a feature of this system rather than shifting agriculture (Mrema et al. 2001), probability of conversion should increase away from rivers. Agricultural plots on higher ground and on steeper slopes are expected to be less-waterlogged and hence to support better crop growth. However, slopes that are too steep or too high may not be as productive as those that are lower down and less steep, therefore the overall effect of slope and elevation on propensity to convert is unclear. Contrasting results on slope and elevation on deforestation have been found (Chomitz and Gray 1996, Deininger and Minten 2002). Soil types were only available at a broad scale: the soil map from which the coverage was derived indicates only three different soil types present at Mabira Forest Reserve (Jameson 1970). To try and capture variation in soil type at a finer scale, I included distance to the nearest agricultural plot and distance from the geographical centre of the forest, assuming that all else equal, those plots already under cultivation should have better soils than those still forested, and by the same logic those plots closer to the heart of the forest will have poorer soils, *ceteris paribus*. These variables may also capture elements of transportation costs that distances to roads and markets do not.

The effect of population growth or density on deforestation has been well-studied, although its empirical effects have varied, and concerns have been raised about collinearity with predictors and reverse causality with deforestation (Angelsen and Kaimowitz 1999). In general, positive effects of population density on deforestation are expected due to increased demand for agricultural land, and an increase in the size of the labour pool, which lowers the cost of labour and hence makes deforestation more financially attractive. Positive effects may also be expected in instances where local markets are important for agricultural products, and hence greater population means a larger market for producers.

I assume that standing forest has no other economic benefit aside from providing habitat for forest birds, and therefore that there are no additional costs to clearing forest other than those mentioned above. This is a potentially serious underestimate of value if non-timber forest products (NTFP's) play an important role in the local economy (Godoy et al. 2001). In the area surrounding Mabira Forest, the major NTFP's collected from the forest were fuelwood and water (Mrema et al. 2001). Most households, however, did not rely on the forest for fuelwood, which is typically one of the most important NTFP's provided by tropical forests (Campbell and Luckert 2002). Only about 25% of households gathered fuelwood from the forest, the remainder either used trees on-farm

(63%), or purchased from their neighbours' farms (12%). In contrast, all households surveyed collected water from the forest. Water is typically among the most difficult of NTFP's to value, however, and accurate quantitative estimates are often impossible to obtain (Campbell and Luckert 2002). I therefore leave these measures of NTFP's out of the value of standing forest, assuming they are either minimal (fuelwood) or impossible to quantify (water). Further research on NTFP collection at Mabira Forest would determine whether this assumption is warranted.

Since I define two states for each plot, the probability A_i that a plot has been deforested can be estimated by a logistic regression model that includes the variables described above:

$$\text{logit}\,[A_i\,(1,0)] = \exp(\beta X_i + \beta_0) \qquad (3)$$

where logit refers to the log-odds transformation of A_i, β is a vector of coefficients on the X explanatory variables, and β_0 an intercept term.

The resultant probabilities of deforestation for spatially referenced plots are relative measures of net economic rent. To move to an absolute measure of economic rent, I multiply probabilities by the average rent G of an agricultural plot in the area surrounding the Mabira Forest Reserve. The average rent was estimated by calculating the product of relative abundance, productivity, and farmgate price of seven main crop types grown by farmers in the Mabira Forest buffer zone (Mrema et al. 2001), and subtracting the average input costs associated with each crop (World Bank 1993). The result for each plot is the expected economic rent, and hence a measure of the cost of supplying avian habitat:

$$R = A_i \times G \qquad (4)$$

To translate economic costs of forest habitat into those for bird species, I used data on avian biodiversity and forest area for 64 protected areas in Uganda (Howard et al. 2000). I constructed a species-area relationship from these data:

$$\text{Log}_e\,(\text{SPP}) = 2.41 + 0.46 \times \text{Log}_e\,(\text{AREA}) \qquad (5)$$

that was highly significant ($F_{57,1} = 52.6$, $P < 0.0001$), with the log of area explaining 50% of the variance in the log of species numbers. I then used this relationship to convert land economic rents into economic rents per bird species, by assuming that: 1) plots of land are deforested in descending sequence according to the economic rent, and hence the cost of conserving bird habitat rise as the number of bird species to be conserved increases; and 2) all forest plots provide equivalent forest bird species habitat, and thus have equal expected values of avian species richness. The total cost curve for avian biodiversity is therefore:

$$S = R \times SPP \qquad (6)$$

where number of species is calculated from (5) and the economic rent from (4).

Data

Data on land-use categories (forested versus converted) were obtained from interpretation of two Landsat satellite images of Mabira Forest and the surrounding area. The first of these was from December 1986 (TM), and the second from December 2001 (ETM). By using images from the same month I hope to have reduced biases due to seasonal variation in forest phenology. I estimated the rate and spatial location of deforestation from 1986 to 2001 by digitizing land-use at a 1:50,000 scale from these two images. Land-use types considered were intact forest, small-holder agriculture, and regenerating forest from pre-1986 deforestation. This latter land-use class arose from a large-scale invasion of settlers into the Forest Reserve in the mid-1970's; by 1988, when the settlers were ejected, about 25% of the forest had been converted to agriculture as the government either encouraged settlement and/or was unable to prevent large-scale conversion (Mupada 1997). Deforestation from settlers had ended by about 1981 (United Nations Environment Programme 2002), and therefore I consider deforestation from 1986-2001 to be different in origin from the "first wave" of settler-induced deforestation.

Ground-truthing from a related study on avian biodiversity and land-use at Mabira Forest Reserve (R. Naidoo, *unpublished data*) ensured accurate translation of features on the Landsat images into on-the-ground land-use types. All three land-use classes were clearly differentiable based on a real-colour image using TM bands 1,2,3, and a false-composite colour image using bands 3,4,5. A GIS coverage of land-use from the National Biomass Project (NBP) of the Uganda Forest Department, derived from SPOT satellite imagery (1989-1992), aerial photography (1995), and extensive ground-truthing (1993-95) facilitated interpretation of the Landsat images. After digitizing polygons of the three land-use types, I converted the coverage into a grid of one-hectare cells (100m x

100m). There were 831 deforested cells, 7006 regenerating cells, and 22,694 intact forest cells. The overall amount of intact forest that was cleared was 3.5% for the 15-year period, for an annual deforestation rate of 0.24%. This is an order of magnitude lower than the 2.2%/yr from 1973-1988, a time period which included the invasion described above (Westman et al. 1989). Of the three land-use classes, I do not consider further the forest regenerating from pre-1986 deforestation. No repeat deforestation was noticeable in these areas, and much of the area is under scrubby invasive vegetation that is unsuitable as forest bird habitat (R. Naidoo, *personal observation*; J.-M. Boffa, ICRAF-Uganda, *personal communication*), and hence not relevant to either the supply or demand of forest bird biodiversity.

Distances from each 1-ha cell to the nearest paved road, road of any type, village or town, large market town (Jinja or Lugazi), and river, were calculated using GIS coverages provided by the Uganda Forest Department. These coverages of roads and rivers were derived using the same methods as produced the NBP land-use layer. Distance to the nearest village/town, and to the nearest large urban market, were calculated from the NBP land-use coverage, which contained an urban/built-up land-use class. Distance to the nearest agricultural edge and the geographical center of the forest were calculated from polygons digitized from the 1986 Landsat image. While the 1986 Landsat image precedes somewhat the NBP coverages, I assume that features from these coverages are representative of those on the ground at the start of the deforestation period I consider. Most roads save for the larger highways were not visible on the 1986 image (partly due to cloud cover and shimmer), however there were very few roads on the 2001 Landsat image that were not on the NBP roads coverage.

For soils and population density, only coarse-resolution data were available for the study area. The soil type at each cell was determined from a soils layer produced by digitizing the 1:1,500,000 map of soils in Uganda (Jameson 1970). Population density was obtained at the sub-county level from the 1991 population census, the closest year to 1986 for which census data were available. There were 8 sub-counties that overlapped Mabira Forest Reserve in 1991 (boundaries have since changed), but the degree of overlap varied, and hence spatial variation in population density within sub-counties that may affect local deforestation could not be captured. The concern is moderated somewhat by inclusion of the distance to the nearest town/village, which represents how close a cell is to the nearest area of high population density.

Slope and elevation were calculated from a coverage of contour lines, again from the NBS. I calculated a Triangular Irregular Network (TIN) from these lines using ArcGIS 8.1 software (Environmental Systems Research Institute, Redlands, CA). From the TIN, I was able to calculate the elevation and slope of each 1-ha cell.

I recognize that spatial autocorrelation among plots may not be entirely captured by the variables I have included in the model. To correct for this, I first ran a logistic regression model including all explanatory variables and examined the residuals for spatial autocorrelation using a correlogram of Moran's I statistic (Legendre and Legendre 1998). Significant autocorrelation existed at a lag of up to 5000m, although correlation coefficients were highest at short lags (100-400 m) and dropped off at greater distances. Considering the tradeoffs between sampling at higher lags and achieving an adequate sample of deforested plots, I chose a lag distance of 200m and randomly sampled 115 deforested cells and 600 intact forest cells, such that pairwise distances of all plots were greater than 200 m. Examination of the residuals from this model indicated that there was no remaining spatial pattern in the data (non-significant Moran's I correlations of 0.02 to -0.03). Because the proportion of deforested to forested cells in this stratified random sample is higher than that of the actual population of cells, I applied a correction factor to the intercept term; coefficients on other variables are not affected by this sampling bias (King and Zeng 2001). A comparison of simple statistics for variables in the regression sample and the overall population of cells is shown in Table 6-1.

Benefits of biodiversity

I estimated the demand for avian biodiversity by surveying international tourists and foreign residents of Uganda on their preferences for biodiversity in the context of visitation to protected forests. A choice experiment assesses preferences by presenting respondents with a number of scenarios in which several discrete options are each defined by a number of attributes, and asking them which option they would choose (Louviere et al. 2000). By structuring the values of attributes among scenarios according to rules of experimental design, the probability of choosing a commodity can be modelled as a function of the attributes. When one of the attributes is price, this allows a monetary valuation of all other attributes in the experiment. Key considerations in designing a choice experiment are the choice set (identification of appropriate substitutes), attribute selection (identification of a set of attributes that realistically describe each alternative), and attribute levels (values of attributes must be realistic, yet the number of levels for each attributes cannot be unlimited, due to constraints of the experimental design process). This approach to stated choice modelling is thought to improve on CV methods by providing a more realistic context that simulates a consumer's actual choice decision (Boxall et al. 1996, Adamowicz et al. 1998). Such models have been successfully applied to a number of environmental research questions, and the reliability of the data, especially as applied to tourism and recreation choices, is considered to be quite high (Carlsson and Martinsson 2001, Haener et al. 2001, Adamowicz et al. 1994).

I presented tourists and foreign residents of Uganda with a choice experiment in which they were asked to choose a protected area to visit, based on a number of attributes reflecting natural amenities at the site, lodging, and cost. The survey was presented to travellers in the departure lounge of Uganda's international airport at Entebbe. This context resulted in a high rate of response to the survey (87%), as travellers had time on their hands and were usually quite willing to participate. The focus was on tourists and foreign residents because park entrance fees for Ugandan citizens are only 18% of those for non-citizens, and therefore the potential benefits transfer is far greater for these groups. I selected Mabira Forest Reserve and two other forested reserves as part of the choice set, and also included an option not to visit any site. The key variables (and their levels) for this study were the entrance fee (5,15,25,40 U.S.$) and the number of bird species likely to be seen at a site (20,40,60,80 species). I modelled the choice probability as a multinomial logit function, while specifying a random parameters logit model (Train 2003) that allows for variation in the coefficients, thus capturing the variability that may be present in respondents' underlying preferences for attributes. I calibrated the model to actual data on visitation to the three forests, and used this calibrated model to predict how changes in price and bird species affect the share of tourists that chose to visit Mabira Forest. The 5-year average of annual tourist visits to the three reserves (T), along with the current entrance fee, were used to simulate total revenues at Mabira Forest Reserve as the number of bird species tourists expect to see rises. More details on these methods can be found in chapter 5.

The total revenue (benefits of biodiversity demand) curve is thus the following:

$$D = P\,(i = \text{Mabira})*R*T \qquad (7)$$

where the economic rent R is equivalent to the entrance fee multiplied by 0.4. This figure is the proportion of revenues that the district administrative office receives from forestry revenue at Mabira Forest, and thus for lack of existing standards on the distribution of revenue from the ecotourism centre, is a realistic departure point. In addition,

$$P\,(i = \text{Mabira}) = \text{EXP}(\beta X_i + \beta_0 + \beta_1 SPP_i) \,/\, \Sigma_j\, \text{EXP}(\beta X_j + \beta_0 + \beta_1 SPP_j) \qquad (8)$$

where β_0 is the calibrated intercept term, X is a vector of variables predicting tourist visitation that are held constant in simulations, β is a vector of coefficients on these variables, j indexes the three sites, and the random and error components are omitted for expositional clarity. Note that this revenue curve assumes that the value of unobserved birds to tourists is nil. I discuss this direct-use framework in a subsequent section.

Potential for market-based conservation

I combined both the revenue curve and the cost curve to estimate levels of biodiversity conservation that are feasible in a market-based setting. As such, the perspective is of a manager (e.g., the Ugandan government) wishing to maximize the conservation of avian biodiversity, subject to the constraint that costs of conservation cannot exceed benefits. In other words, the manager will seek the highest level of biodiversity conservation that can be funded through receipts from ecotourism alone. This level is determined by the intersection of the total cost and total revenue curves. Note that this is a different perspective from that of a profit-maximising agent (such as the local farmers). A profit-maximising agent would seek the highest profit available from the system, which would be determined from the intersection of the *marginal* supply and demand curves. The underlying philosophy behind this approach is that local stakeholders must be compensated for their opportunity costs of not converting forest to agriculture, but that the goal is to conserve economically feasible levels of avian biodiversity, not to profit from them.

Given that land-use and policy conditions at the Forest Reserve are both fluid, and that many of the parameters used to estimate both supply (opportunity cost) and demand can reasonably be expected to depart in the future from current levels, I conducted some simple comparative statics to estimate how changes in the supply and demand curves might change the market supply of biodiversity. Specifically, I calculate new states given an upward shift in both the supply and demand curves, assuming a time horizon from 2002 of 15 years (equivalent to the period length for which I calculated the current deforestation patterns: 1986-2001). The shift in the total cost curve is based on continued deforestation due to an increase in population density equivalent to the current rate of population growth in Mukono district (3.4%) and on the current distance of forest plots to the nearest agricultural plot. The shift in the total revenue curve is assumed due to a fee increase from 5$ - 47$ U.S. This is the revenue-maximising fee identified from analyses in Chapter 5. I also optimistically assume 100% of revenue is available for distribution to the community; i.e., that maintenance costs at the reserve are nil.

6.3. Results

Agricultural land values

Table 6-2 shows the model of deforestation probability at Mabira Forest, based on the spatial location of plots converted from forest to agriculture from 1986-2001. Most of the variables were significant explanators and in the expected direction; only distance to the town of Lugazi and distance to the nearest river were not significant at the 5% level. Measures of market connectedness (distance to the nearest town/village, Jinja market town, and nearest road of any kind) were significant and negative, indicating sites closer to markets were more likely to be deforested than those further away. This was also true of distance to the forest's geographical center, with plots closer to the center having a lower probability of deforestation, and distance to the closest agricultural plot, which exerted a strong positive effect on probability of deforestation. The exception was distance to the nearest highway, which was significant but positive, suggesting that forested sites further from highways were more likely to have been deforested. This may indicate that the "good" forested areas near the highway had already been deforested prior to 1986, hence the remaining forests close to highways may be unattractive/unsuitable for agriculture due to factors not captured by the model.

Biophysical features were also important predictors of deforestation. Dummy variables for two types of Ferrisols (Ka, Kb) both had positive effects on the probability of deforestation, as compared to the omitted dummy for Ferralitic soil. Ferrisols are in a less-advanced state of weathering than Ferralitic soils, and therefore possess greater amounts of minerals and have better agronomic properties than Ferralitic soils (Jameson 1970). Sites further away from rivers were more likely to be deforested that those nearer to rivers. This may arise because of overly-wet conditions near rivers, or also because of recognition on the part of villagers that maintaining a forest buffer around rivers reduces sedimentation and thus enhances water quality. Lower-elevation plots were more likely to be deforested than higher-elevation plots, while plots having steeper slopes were more likely to have been deforested than those on flat terrain. Population density in 1991 was positively related to probability of deforestation, a consistent finding with the majority of the literature (Angelsen and Kaimowitz 1999).

The average economic rent of one hectare of land, based on returns to agriculture, was estimated at 114$ U.S/yr. Multiplying this value by the modelled deforestation probabilities produced the map of land values for Mabira Forest (Figure 6-1). Higher land values tended to be clustered around the edges of the forest and particularly in the fragmented southwestern part of the reserve, where deforestation has been highest. The unfragmented central and northern parts of the reserve are much less valuable, suggesting effective protection of the reserve's biologically-valuable core can be obtained for a relatively low price.

Biodiversity preferences of tourists

Table 6-3 shows the coefficients for a random parameters multinomial logit model of tourist visitation rates to protected forests in Uganda. Attributes representing lodging facilities (cabins, luxury lodges), landscape features (secondary forest, both primary and secondary forest), chance of seeing large wildlife, and whether the trip was part of a tour, distance to site, and entrance fee were all significant predictors of tourist visitation rates. The natural logarithm of the number of bird species likely to be seen at a site had a strong positive effect on the probability a tourist would visit Mabira Forest. Significant variation in tourist response to distance to site, entrance fee, and bird species was also detected.

I used this model to predict the total revenue accruing to the Mabira Forest ecotourism centre by specifying an entrance fee (the current 5$ U.S.), and then simulating the proportion of visitors choosing Mabira over the other two forest choices as the number of bird species seen at Mabira Forest increased. The total revenue was calculated by multiplying this proportion by the total pool of visitors that visit the three sites on an annual basis (3765 on average over the last 5 years) and by the entrance fee. This gave the total annual demand for avian biodiversity at Mabira Forest. More details on results are in Chapter 5.

Potential for market-based conservation

Figure 6-2 shows the level of avian biodiversity at Mabira Forest Reserve that would occur given current market conditions. The total cost curve increases slowly then curves upward rapidly, indicating that the cost of supplying the majority of bird species is low, but increases sharply towards higher numbers of species. The total revenue curve also increases but at a decreasing rate, indicating that the value of individual bird species to tourists decreases as the total number seen rises. The intersection of these two curves is the point at which further increases in numbers of bird species can no longer be "funded" solely through tourism. For avian biodiversity at Mabira Forest, this point (S_0) is at 114 bird species[15]. As the forest is currently estimated to contain 143 forest bird species[16], this market-based model of avian biodiversity predicts a "surplus" of 29 bird species that could not be conserved by market conditions alone.

Future changes in variables that determine the supply-demand relationship of birds at Mabira Forest are likely. Figure 6-3 shows shifts in biodiversity states away from S_0 with various change scenarios. Curve TS' shows cost increases related to population growth and high probabilities of deforestation adjacent to agricultural areas.

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[15] I round off to the nearest bird species for all supply points.

[16] While 287 species are on the Mabira Forest Reserve bird list, only 143 of these are considered forest dependent. The remainder are associated with wetlands, or with the agricultural enclaves that are within the reserve's boundaries.

The intersection with current revenue (TD) is at 113 species, indicating almost no change in biodiversity level with this scenario. In contrast, increases in demand due to a fee increase to the revenue-maximising level (curve TD') result in biodiversity levels of 131 species (intersection with current conditions curve TS) or 127 species (intersection with curve TS'). Curve M represents the total costs assuming a land value of 114$ U.S. for every hectare in the forest reserve. This could be thought of as the cost of reforesting agricultural land to provide forest bird habitat. Although this is unlikely to be ecologically feasible, the curve illustrates that it would also be economically infeasible for most bird species: less than ten species could be conserved through tourism receipts if land prices were this high.

6.4. Discussion

The demand-side economics of biodiversity conservation have been little-studied, compared to supply-side costs. One possible reason is that markets for biodiversity may not exist, or be so severely distorted that prices do not reflect true value. Market failure is well-known for cases of environmental goods, and can occur in situations when property rights are ill-defined and/or consumers are ill-informed of the benefits of the good in question (Perkins et al. 2001). Both of these certainly apply to the global biodiversity market, however, the world's biodiversity is being reduced through localized extinctions in many disparate regions throughout the world, with the loss of populations of species at finer scales perhaps the first step in biodiversity loss (Hughes et al. 1997). At these disaggregated levels, local markets for aspects of biodiversity that are in demand may have a role to play in wider conservation efforts.

I contend that such a market could exist for biodiversity at Mabira Forest reserve. Avian biodiversity, the surrogate measure for overall biodiversity, is significantly correlated with butterfly biodiversity and large moth biodiversity in Ugandan forests, and correlation between bird and mammal species richness is marginally significant (Howard et al. 1998). Therefore if preferences for the conservation of elevated levels of avian biodiversity do exist, they should benefit other taxonomic groups as well. Birds are also a well-known aspect of biodiversity: all survey respondents had surely seen birds before, and thus information regarding this aspect of biodiversity is high. Realistic decisions regarding the value of observing a certain number of bird species is thus likely to be high, particularly in relation to other less visible or highly obscure taxonomic groups.

On the supply side, compensation for local people's foregone access to forest resources is well-recognized from legal and moral perspectives (Colchester 2000). More pragmatically, it has been suggested that without the active participation or acceptance of local people, who are often the best (or at least defacto) custodians of natural resources, conservation programs are destined to fail. This view, however, has been the subject of fierce debate (Redford and Sanderson 2000, Schwartzman et al. 2000). My approach abstracts from this and simply assumes that local farmers respond to economic conditions by assigning the land-use of highest value to a plot of land. Should the net economic rent of a plot of forest exceed the value of the plot as agriculture, it will be conserved, otherwise, it will be cleared. Empirical support for this view of farmers as utility-maximizing agents is found in the econometric deforestation literature (Angelsen and Kaimowitz 1999, Chomitz and Gray 1996, Deininger and Minten 2002, Pfaff 1999). This type of stylized representation of the land-use decision allows a clear assessment of the economic incentives to deforest versus conserve, producing quantitative predictions on market incentives for conservation, and economic values of biodiversity that are relevant to both the decision-maker and the policy-maker.

This approach to determining the optimal level of biodiversity focuses on direct-use values, in contrast to much of the environmental valuation literature that concentrates on passive use values (Costanza et al. 1997, Loomis and White 1996). I argue that in many developing country contexts, the direct-use framework for valuation of biodiversity is the appropriate one to use. Passive-use values, while often shockingly large, bear little relation to actual economic decision-making unless they can be captured by the relevant agents (Pearce 1996). In the case of Mabira Forest Reserves, redistribution of proceeds from the ecotourism centre offers a realistic incentive to smallholders to preserve forest rather than clear it for agriculture. Estimates of the size of economic shortfall that may need non-market intervention can be made for the conservation of a given level of biodiversity. Market analyses of biodiversity could also be conducted at the growing number of private reserves in the tropics (Langholz and Lassoie 2001), to determine whether preferences for biodiversity are economically significant reasons for visitation.

This is a practical alternative to trying to estimate a value for the global benefits of any one target area, with all the inherent problems of identifying a reference population, dealing with information deficits, selecting appropriate valuation attributes, and eliciting a realistic response.

The estimates of the economic value of biodiversity that are presented here are much lower than several recent high-profile valuation studies for other environmental goods and services (Costanza et al. 1997, Pimentel et al. 1997, Balmford et al. 2002). The economic methods and assumptions used in these types of studies have been strongly criticized (Bockstael et al. 2000). However, the larger issue that arises from this research is: how can a large willingness-to-pay for ecosystem goods and services, on the part of the global public, be translated into effective conservation action? For this to occur, the economic benefits afforded to society at large must somehow be transferred to people who will bear the opportunity costs of conservation. These are often local, impoverished populations similar to the those living on the margins of Mabira Forest Reserve. Pearce (1996) addressed this issue and showed that global benefits of tropical forest preservation are likely to be high, and that institutions to capture this value are possible, particularly through international markets such as that for carbon credits. However, the political obstacles to implementing the Kyoto Protocol and associated carbon emissions markets are an indication of the difficulties in developing international markets for passive use values. An international market for biodiversity would in all likelihood pose many more problems than one for a "straightforward" environmental good such as carbon. Local markets, such as the one possible at Mabira Forest, should be easier to create, and will still retain aspects of international benefits transfer by virtue of foreign tourist expenditures.

Given the spatial distribution of land rents at Mabira Forest Reserve, it is likely that without even nominal protection afforded the area through its forest reserve status, a significant chunk of the area would be further converted to agricultural land, although low land values in the reserve's core would persist for some time. Continued non-market intervention to reduce land values or enforce the reserve's boundaries is therefore needed if all forest bird species are to be conserved. Nevertheless, with the continued protected status of the reserve, current annual tourism receipts of 9,500$ U.S. are enough to offset the opportunity costs of conserving 114 of 143 avian species. In addition, the model suggests that increasing fees to revenue-maximising levels and completely redistributing receipts to the surrounding community would further increase the number of species afforded habitat protection, up to 131 species. On the other hand, if land values throughout the forest reserve were as high as those in surrounding agricultural areas, conservation of all but a handful of species would be economically prohibitive. As such, prevailing conditions currently offer a "window of opportunity" to achieve economically feasible conservation of the largest remaining habitat patch for forest birds in southern Uganda.

While market forces are generally assumed to significantly underestimate the value of biodiversity, I have shown here that 80-90% of a remnant rainforest's avian biodiversity could be protected through current market conditions. I suggest that case studies of potential biodiversity markets in tropical developing countries, where species diversity is often high and land prices relatively low, could provide policy-makers with quantitative estimates of the possibility of market solutions to biodiversity problems.

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6.6. Tables

Table 6-1. Variables used in logistic regression analysis of deforestation during 1986-2001

		Entire study area					Sample for regression model				
Variable*	units	*n*	Mean	Std Dev	Min	Max	*n*	Mean	Std Dev	Min	Max
road_dist	m	23,526	1,535	1,188	0	5,192	654	1,420	1,141	0	4,753
hwy_dist	m	23,526	7,283	3,586	0	14,269	654	7,224	3,519	0	14,052
urban_dist	m	23,526	5,424	2,395	0	10,875	654	5,144	2,466	200	10,617
jinja_dist	m	23,526	27,866	6,365	11,871	41,623	654	28,349	6,656	12,467	41,615
lugazi_dist	m	23,526	14,490	3,992	5,544	24,313	654	14,252	3,890	6,174	24,203
river_dist	m	23,526	394.6	318.2	0	2,022	654	372.6	308.9	0	1,526
slope	degrees	23,526	8.98	10.95	0	78	654	8.97	11.3	0	60
elev	feet	23,526	3,748	158.2	3,545	4,378	654	3,746	156.4	3,548	4,339
bound_dist	m	23,526	759.4	703.4	0	3,667	654	706.5	693.1	0	3,492
centroid_dist	m	23,526	7,566	3,659	0	18,522	654	7,899	3,905	100	18,449
ka	-	23,526	0.24	0.42	0	1	654	0.21	0.41	0	1
kb	-	23,526	0.15	0.35	0	1	654	0.14	0.35	0	1
popdens91	inds/km^2	23,526	127.9	40.6	11.1	503.4	654	131.7	49.2	90.8	503.4

* Variable definitions: road_dist = distance to the nearest road; hwy_dist = distance to the nearest highway; urban_dist = distance to the nearest urban centre; jinja_dist = distance to the town of Jinja; lugazi_dist = distance to the town of Lugazi; river_dist = distance to the nearest river; slope = slope in degrees; elev = elevation in feet; bound_dist = distance to nearest administrative boundary of Mabira Forest Reserve; centroid_dist = distance to the geographical centre of the forest; ka = dummy variable for undifferentiated Ferrisol; kb = dummy variable for crystalline basic Ferrisol; popdens91 = human population density in 1991

Table 6-2. Logistic regression results for deforestation at Mabira Forest Reserve, 1986-2001

Variable	Coefficient	Std Error	Chi-square	*P*-value	Standardized B
Intercept	21.1	10.4	4.10	0.043	-
road_dist	-0.00062	0.00028	4.97	0.026	-0.39
hwy_dist	0.00021	9.5E-05	4.78	0.029	0.40
urban_dist	-0.0004	9.9E-05	16.4	<.0001	-0.54
jinja_dist	-0.00026	9.4E-05	7.41	0.0065	-0.94
lugazi_dist	-0.00007	0.00012	0.36	0.55	-0.15
river_dist	0.0010	0.00064	2.39	0.12	0.17
slope	0.040	0.0143	8.04	0.0046	0.25
elev	-0.0049	0.0023	4.53	0.033	-0.42
bound_dist	-0.0038	0.00069	31.0	<.0001	-1.46
centroid_dist	0.00030	0.00013	5.70	0.017	0.65
ka	0.73	0.38	3.73	0.053	-
kb	1.09	0.52	4.31	0.038	-
popdens91	0.010	0.0038	7.59	0.0059	0.28

$n = 654$

% deviance explained = 43%

-2 Log-likelihood = 262.9

Likelihood ratio chi-square = 262.9, df = 13, $p < 0.00001$

Table 6-3. Random Parameters Logit regression results for visitation rates to forest reserves.

Attribute	Coefficient (SE)	*t* - Value
Random parameter means		
ln (Birds)	0.66 (0.027)	24.4
Entrance fee	-0.025 (0.002)	-12.5
ln (Travel time)	-0.047 (0.074)	-0.63
Random parameter standard deviations		
ln (Birds)	0.77 (0.029)	26.7
Entrance fee	0.040 (0.002)	18.9
ln (Travel time)	2.36 (0.098)	24.1
Non-random parameters		
Part of tour	-0.073 (0.017)	-4.1
Tents	-0.024 (0.034)	-0.7
Cabin	0.37 (0.032)	11.4
Luxury lodge	0.15 (0.028)	5.3
Primary forest	-0.018 (0.032)	-0.6
Secondary forest	-0.15 (0.033)	-4.5
Both forest types	0.077 (0.027)	2.8
Chance of wildlife	0.68 (0.019)	35.0
Log-likelihood	-11,707	
Pseudo R^2	0.38	
Number of observations	13,623	

6.7. Figures

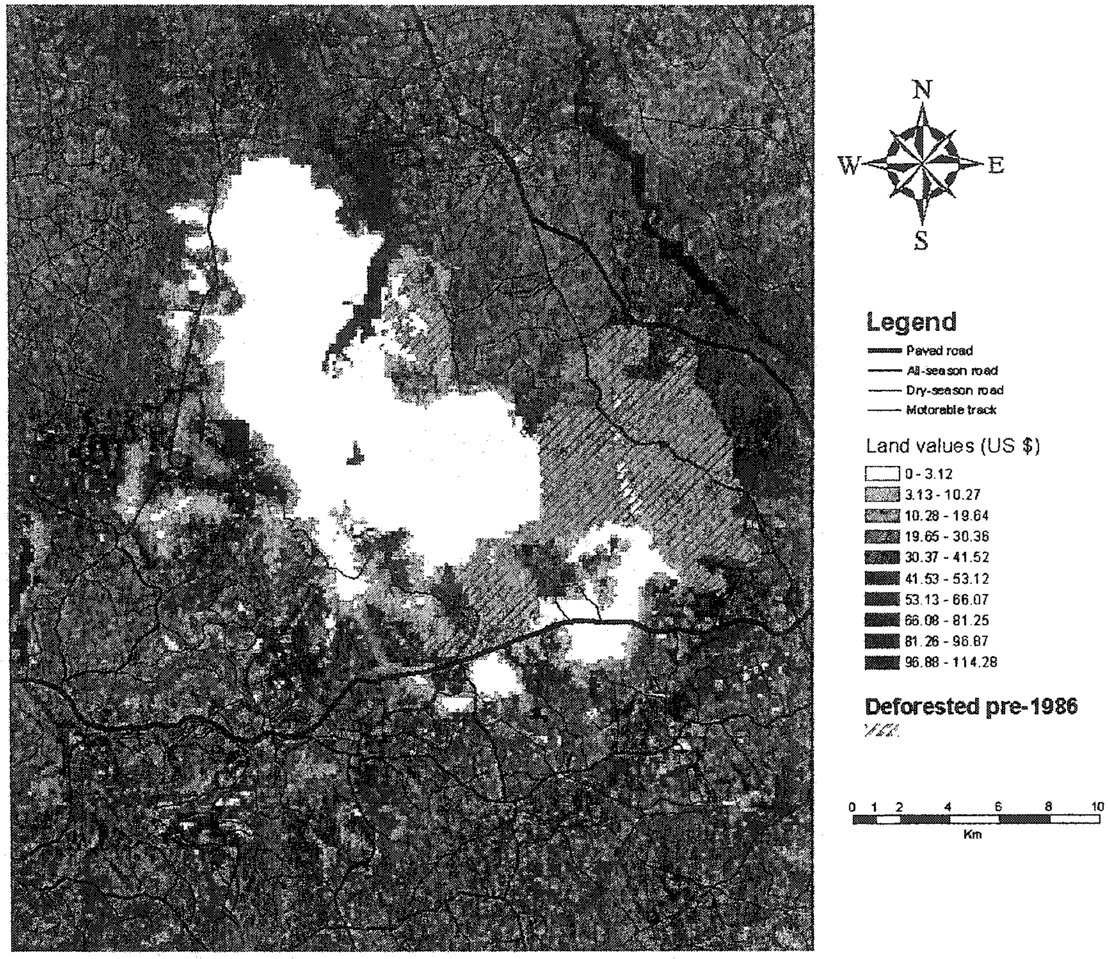
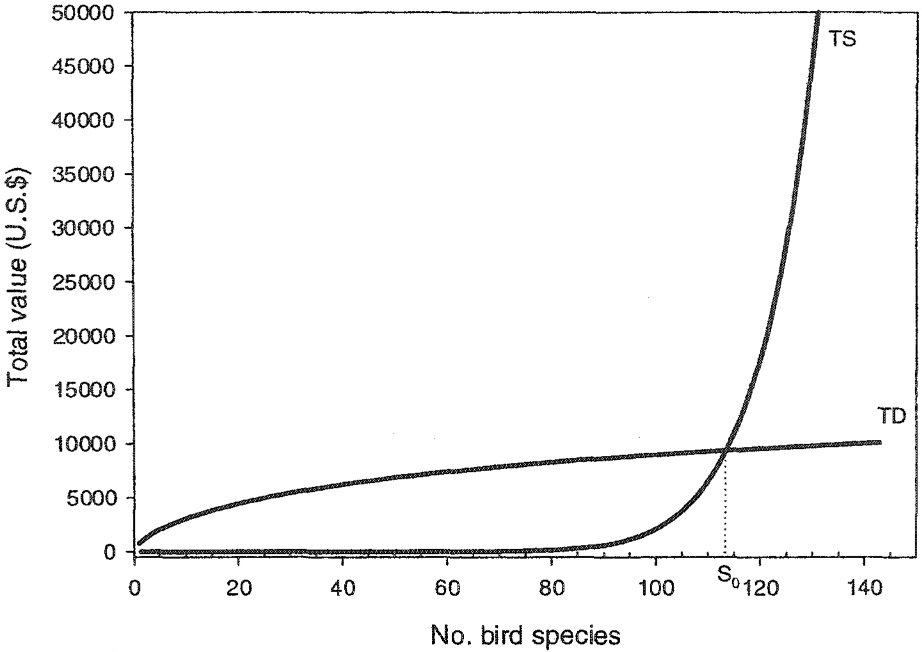


Figure 6-1. Land rents for Mabira Forest Reserve, 2001 U.S.$. Darker areas indicate higher land rents. The local road network is also shown, as well as a grayscale Landsat image of the surrounding landscape. Stippling indicates areas deforested prior to 1986, now regenerating.



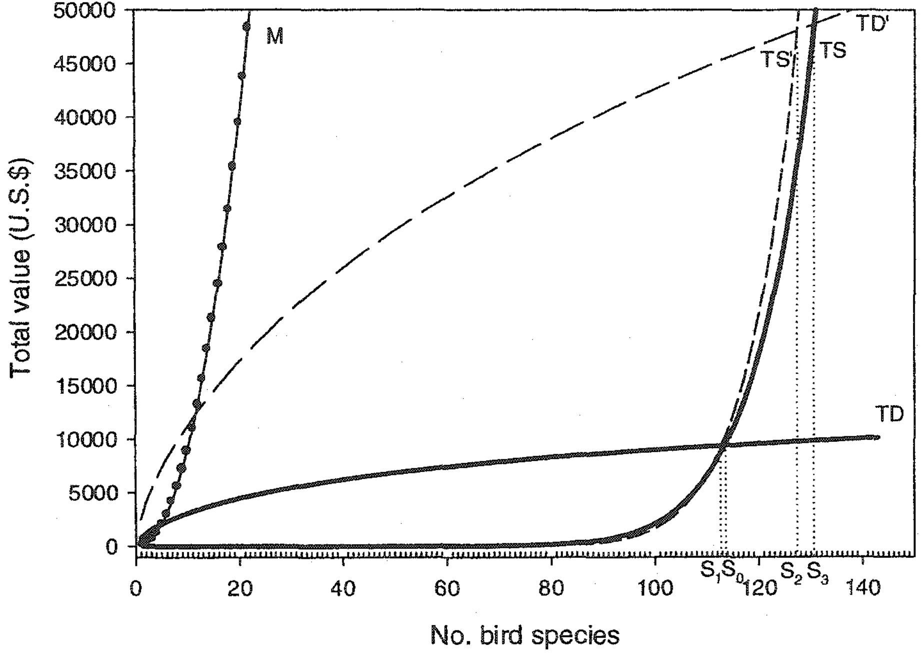


Figure 6-2 (upper panel). Total cost – revenue curves for avian biodiversity conservation at Mabira Forest Reserve. TS – total cost curve; TD – total revenue curve; S_0 – maximum feasible supply of forest bird species.

Figure 6-3 (lower panel). Total cost – revenue curves under various scenarios for avian biodiversity conservation at Mabira Forest Reserve. TS – cost curve; TD - revenue curve; TS' – cost curve shift; TD' – revenue curve shift; S_0 – current supply of forest bird species; S_1 – supply under least favourable scenario; S_2 – supply with both supply and demand shift; S_3 – supply under most optimistic scenario. M – cost curve with land values at a constant 114$ U.S.

7. General Conclusions

Large-scale results

Chapter 2 showed that increased economic prosperity was correlated with higher numbers of threatened species for four taxonomic groups: plants, reptiles, amphibians, and invertebrates. Two groups showed no relationship (fish and mammals), while for birds, evidence of an EKC relationship was found. While I did not investigate possible mechanisms to explain these findings, three sets of factors may combine to determine general relationships between measures of environmental quality and per-capita income: preferences, technology, and institutions.

Anecdotal evidence suggests that a greater preference for birds than other taxonomic groups may be at least partly responsible for the EKC pattern I observed (Metrick and Weitzman 1996, Simon et al. 1995). Increased education and awareness of other taxonomic groups may therefore be important strategies to develop stronger preferences for a wider variety of organisms among society at large. Technology is often cited as an important factor in explaining why pollution levels may decrease at higher-income levels (Andreoni and Levinson 2001). For biodiversity, technology appears unlikely to contribute to reductions in pressure as income grows, because the most effective conservation solutions often require less human intervention, not more (i.e., the protection of large areas of intact habitat). Finally, appropriate institutions are necessary to translate increased preferences, or the development of new technologies, into actual conservation action. It is possible that current institutions that aim to alleviate threats to species, such as the U.S Endangered Species Act, are biased towards more charismatic taxa such as birds (Metrick and Weitzman 1996, Simon et al. 1995), and therefore are less able to contribute towards conservation of less-charismatic taxa. More research on how these mechanisms apply to threatened species is necessary. In the interim, most relationships between numbers of threatened species and economic prosperity offered no support for the EKC hypothesis. Assuming that numbers of threatened species' numbers are a suitable proxy for the threat to biodiversity, and that underlying factors producing the patterns in Chapter 2 remain stable through time (a strong assumption), pressure on biodiversity will increase as per-capita incomes continue to rise.

Similarly pessimistic conclusions result from the analysis of Chapter 3. Here I showed that liquidation of natural capital has been an important contributor to recent economic growth over a large cross-section of countries. These countries spanned a range of income levels, original forest endowments, and geographical localities. Models including these factors and a number of traditional predictors of national growth rates did not change the basic positive relationship between amount of forest cleared and economic growth. Therefore, natural capital has not been preserved as countries develop faster. The opposite has in fact occurred, with countries that have liquidated more of their natural capital experiencing higher economic growth rates. To the extent that clearing of forests represents a loss of biodiversity, the policy goal of attaining high economic growth has not benefited biodiversity, but has rather occurred at its expense.

It is interesting that the results of two quite different analyses, one examining the effects of absolute per-capita income (Chapter 2), and the other effects of *growth* of income (Chapter 3), both show little support for the environmental Kuznets curve hypothesis. I am therefore doubtful that economic growth and increasing per-capita incomes will spur increased environmental quality, as several authors have forcefully argued (Lomborg 2001, Beckerman 1992), at least with regards to biodiversity conservation. These results are especially unsettling for the tropics, where the majority of the world's species exist and where poverty and under-development are most acute. It underscores the need for an understanding of why the patterns of Chapter 2 occur, in the hope that mitigative strategies can be designed such that increasing income can lead to reduced, not increased, pressure on biodiversity. It also suggests that given the multitude of possible indicators of environmental quality, a general relationship between increasing economic prosperity and environmental quality is unlikely to exist. Policy recommendations should therefore not assume such a relationship will occur (Lomborg 2001, World Bank 1992). Finally, these results indicate that at the country-level, the economic benefits of converting forests have exceeded benefits from their conservation. Recent studies showing that forests may actually have higher economic value if left unconverted (Kremen et al. 2000, Adger et al. 1995) suggest that these benefits have not been captured by the relevant decision-making agents, a point to which I return in the following section.

Case study results

Threats to the environment at Mabira Forest Reserve in southern Uganda are typical of those in many developing countries. Having already degraded much of the natural environment, pressures from an increasing population that is mired in poverty threaten remaining natural resources whose existence continues only through some form of government protection. In such situations, a range of sustainable development policy options may be considered. Continued funding from governments or international donors may be sought, although such sources can be difficult to find and may encourage local dependency. Environment-enhancing interventions that mitigate degradation and reduce pressure on natural resources, such as agroforestry in buffer zones surrounding protected forests, have been heavily touted. Conservation policy derived from the development of new markets for renewable natural resources is an option which conservationists are often uncomfortable with. I examined examples of each of these policy options, with somewhat surprising results.

Firstly, I surveyed avian species richness and community structure in Mabira Forest and in the surrounding "buffer zone", an area of subsistence farming where NGO-sponsored agroforestry programs are underway (Chapter 4). The results suggest that forest bird species are largely restricted to the reserve itself; few forest bird species were found in small-scale farming habitats, and community structure between forest and non-forest was very different. These results are at odds with recent studies that suggest small-scale agricultural habitat may contain larger numbers of forest species than was previously thought (Ricketts et al. 2001, Daily et al. 2001). They also cast doubt on the proposed "win-win" benefits of agroforestry, since the degree of tree-planting required to raise tree densities to levels beneficial to forest biodiversity would almost certainly conflict with crop production, and are therefore unlikely to be adopted. Tree – planting may still reduce pressure on the reserve's forest resources, and therefore should continue to be explored as a way of reducing forest degradation. It should not be expected to contribute directly to forest bird conservation in this system, however.

Secondly, an experimental assessment of tourist preferences for protected areas showed that the chance of seeing higher numbers of bird species would lead to increased visitation rates of tourists visiting forest reserves in Uganda (Chapter 5). By providing economic evidence of increased value for higher levels of biodiversity *per se*, (e.g., the number of different species in an area), this powerful result shows that economic rationale for biodiversity preservation may exist at a market level. Previous research on related environmental goods and services has mostly focused on elusive passive-use values (Pimentel et al. 1997, Costanza et al. 1997). However, we must be cautious about extrapolating inferences regarding market effectiveness of biodiversity preservation. I have already shown that conservation preferences for birds, a highly visible and taxonomic group, may exceed those for other types of organisms (Chapter 2). In addition, although avian biodiversity is a reasonable surrogate for overall biodiversity in Ugandan forests (Howard et al. 1998), this is not usually the case (Lawton et al. 1998), and therefore demand for high avian diversity areas will not necessarily result in the protection of areas high in overall numbers of species. Finally, an evaluation of the possibility of market-based biodiversity conservation must include not only the benefits, but also the costs of provision, an issue which I addressed in Chapter 6, and which I now summarize.

I integrated results from Chapter 4, Chapter 5, a GIS analysis of land values in the Mabira Forest Reserve, and a published species-area curve for Ugandan forest birds (Howard et al. 2000), to determine how local markets may contribute to the conservation of biodiversity at Mabira Forest (Chapter 6). This indicated that at current (admittedly low) deforestation rates, protection of the avifauna due solely to tourist demand for bird species would result in the retention of 114 of 143 forest bird species. Other scenarios covering a likelihood range of pessimistic to optimistic show that market-based conservation programs would conserve 80-90% of the forest birds at Mabira Forest. The extirpation of any species must be considered a conservation failure, and by this definition market forces alone cannot successfully conserve the reserve's avian biodiversity. Nevertheless, a market-based conservation program would not result in catastrophic species losses. In contrast to passive-use values that have little relevance to actual economic decision-making in the absence of global institutions, this direct-use value is meaningful in a conservation and development policy context. Actual dollar values necessary to effect a change in human behaviour are identified. The successful implementation of a program like the one described above will depend upon the emergence of appropriate institutions, and is a critical area for future research.

Synthesis – economics, biodiversity, and sustainable development

While there is no shortage of rhetoric on the prospects for sustainable development, meaningful policy options *should* be developed on the basis of the best available scientific information from a variety of disciplines. I hope to have contributed to the scientific literature on sustainable development by assessing how economic analyses can offer insights into the conservation of biodiversity. Readers hoping for an unambiguous message on how economic behaviour shapes our effects on the natural world will likely be disappointed with the following conclusions, however. First, the majority of the analyses using cross-country data suggest that economic growth is not a panacea for conservation. The liquidation of forests has long contributed to national economic growth; given the continuing emphasis on increasing per-capita incomes as rapidly as possible, incentives to conserve this natural capital are probably low. Numbers of threatened species generally increase with increasing national per-capita income, thus the richer a country, the greater the number of species that are at risk of extinction. At the macro-level, then, it appears that policies advocating economic growth and biodiversity conservation run counter to one another, with little prospect of a win-win situation. A glimmer of hope, however, is contained in the results for birds and per-capita income; if we can understand why this pattern exists, perhaps relationships for other taxonomic groups can be changed.

I find more reason for optimism from the localized studies of Chapters 4 and 5. Foreign tourists in Uganda show a marked preference for more bird species rather than fewer, all else equal. This demand for biodiversity is almost enough to offset the status quo costs associated with protecting all remaining forest bird species in an area of high human population density and extreme poverty. This result shows that not all economic behaviour need be harmful for the environment. Perhaps by encouraging the development of localized "biodiversity markets" such as this one, some small steps towards conservation of global biodiversity can occur, such that ultimately the macro-level patterns of threatened species begin to resemble those for birds. Further research in this area is strongly encouraged.

Finally, Colin Clark, the noted UBC economist, once wrote that "Individual rationality, in complete contrast to the case of resource shortages, encourages rather than discourages degradation of the environment...No previous civilization has survived this dilemma, and there is as yet little evidence that our present industrial civilization will succeed in doing so."[17] It is my sincere hope that this thesis provides both an illustration of the large-scale environmental degradation we have caused, and an example of how local economic processes may nevertheless contribute to a sustainable future.

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[17] In addition to the above quote, he provides a summary of the open-access nature of environmental degradation in Clark, C.W. 1995. Scale and the feedback mechanism in market economics. Pages 143-148 *in* Swanson, T.M., editor. The economics and ecology of biodiversity decline. Cambridge University Press, Cambridge, UK.

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