THE ECONOMIC IMPLICATIONS OF A MULTIPLE SPECIES APPROACH TO BIOECONOMIC MODELLING

A thesis presented in partial fulfilment of the requirements for the degree of Master of Applied Economics at Massey University, Palmerston North, New Zealand.

Christopher Mark Fleming

2002

ABSTRACT

Human activity frequently leads to the endangerment or extinction of other species. While ecologists study the biological facets of species loss, economics, as the science of understanding people's behaviour, has been charged with investigating the incentives underlying the actions people take that lead to this loss. One approach economists have taken to gain this understanding is to develop models of endangered species that include both economic and biological components, known as bioeconomic models. While ecologists frequently note the importance of modelling entire ecosystems rather than single species, most bioeconomic models in the current literature focus only on a single species. This thesis addresses the economic significance of this assumption through the development of a series of multiple species models and demonstrates, using African Wildlife as an example, the importance of interrelationships and economic values to the survival of endangered species.

From these models one can infer the conditions under which a single species model may be appropriate, at least in general terms. If species are independent, and either the opportunity cost of capital or the value of habitat is very low relative to the value of the species in question, then a single species model may yield results similar to that of a multiple species model. In contrast, if species are independent and these additional conditions are not met, a single species model may significantly underestimate both optimal stock levels and land allocation.

However, species do not live independently; they interact with species with which they share habitat and, when species interact, the potential for misapplication of the single species framework is even greater. When species compete, the single species framework consistently produces higher stock levels than the multiple species framework, the greater the level of competition the greater the difference. In a predator-prey relationship, the relative values of predator and prey are critical to determining the outcome of the multiple species model.

It is demonstrated that the inclusion of at least all economically valuable species in an ecosystem is important when constructing bioeconomic models. Using single species models where multiple species are economically significant could lead to misleading results and ultimately to incorrect policy decisions.

ACKNOWLEDGEMENTS

I would like to acknowledge the following people for helping to make this thesis a reality:

Dr Robert Alexander to whom I am greatly indebted for stimulating my interest in this area and providing guidance throughout the research process.

Graeme Doole for his assistance with the use of GAMS and his valuable comments on the thesis as a whole.

Sheila Alexander and Rachel Leong for their contribution to the final editing.

The Leong family for providing a home away from home and offering support and encouragement.

Finally, I would like to thank my family for their ongoing and invaluable support.

TABLE OF CONTENTS

LIST OF APPENDICES

LIST OF FIGURES

CHAPTER I

INTRODUCTION

1.1 Background and Objectives

As we begin the twenty-first century, the earth faces unprecedented levels of species loss. The World Conservation Union's (IUCN) Red List of threatened species currently contains in excess of 11,000 species of plants and animals, including 24 percent of mammal and 12 percent of bird species, all facing a high risk of extinction in the near future. In the four years from 1996 to 2000, the total number of threatened animal species has increased from 5,205 to 5,435 (IUCN, 2000).

Although species extinction is by no means a new phenomenon, this current 'wave' has a crucial distinction from those that have come before - the cause is anthropogenic in origin. Human activity, whether through deliberate exploitation, conversion of habitat, or the introduction of new species, has undeniably led to a decline in the number of species in existence. In fact, in the last 500 years, human activity has forced 816 species to extinction (103 since 1800), suggesting a rate of extinction some 50 times greater than would occur 'naturally'. Moreover, given the large numbers of species that remain unidentified (many species are lost before they are even discovered), these estimates are generally considered to be low (IUCN, 2000).

The loss of a species represents the loss of an opportunity. Once extinct, any potential use of that species, whether as a cure for disease, a source of food, or simply a source of appreciation, is gone. Species such as the Rosy Periwinkle *(Cantharanthus roseus)*, a plant from the tropical-dry forest of Madagascar (a key component in the treatment of Hodgkin's disease and childhood leukemia), have the potential to yield significant financial (and social) returns. Estimates suggest up to 80 percent of the world's health problems are treated by plant-based medicines, making the preservation of species not simply an altruistic concern, but a selfish one, directly contributing to our own wellbeing (IUCN, 2000).

Leading the way in the study of species loss is the field of ecology. Ecology emerged as a sub-discipline of biology in the early 1970s and can be defined as '...the scientific study of the interactions that determine the distribution and abundance of organisms' (Krebs, 1972, p.7). Ecology deals with three levels of concern: the individual organism, which addresses how individuals are affected by (and how they affect) their biotic and abiotic environment; the population (consisting of individuals of the same species), which deals with the presence or absence of particular species, with their abundance or rarity, and with the trends and fluctuations in their numbers; and the community (consisting of a greater or lesser number of populations), which deals with the composition or structure of communities (Begon, et al., 1996).

In the early development of ecology, the sheer complexity of natural communities seemed to preclude analysis at the community level of organisation. Early quantitative studies focused on individual species, namely the population dynamics of single species populations; studies at the community level of organisation were for the most part purely descriptive. However, since the late 1960s there has been significant progress in the study of ecology at the level of whole communities. The development of sophisticated modelling techniques and computer programs capable of handling the complexity of interaction, together with increased rigour of analysis of field observation, have all led to widespread advances in understanding the structure and composition of ecological communities. In the discipline today it is almost gratuitous to note that any single species population exists not in isolation, somehow separable from the complexity of interactions around it, but as an integrated component within a greater 'whole' (Putman, 1994).

As the understanding of ecological communities has grown, so too has criticism of conservation efforts. Conservation efforts have traditionally focused upon the identification and preservation of a small number of charismatic species, and in many cases upon deliberate overexploitation by human beings as the cause of endangerment. The plight of species such as the White Rhinoceros *(Ceratotherium simum)*, the Giant Panda *(Ailuropoda melanoleuca)* and the Blue Whale (*Balaenoptera musculus*) are well documented and (comparatively) well funded. While these concerns remain valid, as our knowledge of the many and varied interactions among species, their habitat, and the environment has improved, the perception of the nature of the problem of species extinction has shifted. The issue of species loss has become a broader concern, a concern that includes the potential loss of millions of unknown life forms (Swanson, 1994).

The last 30 years have seen the development of a significant body of literature surrounding the conservation of ecosystems as opposed to single species. The terms 'biological diversity', or 'biodiversity',[1] have become commonplace, and conservation catchphrases have turned from 'Save the Whale' to 'Save the Planet'. This new focus culminated in the 1992 signing of the Convention on Biological Diversity (CBD), a global convention, a central tenet of which is the 'conservation of biodiversity' (United Nations Environment Programme (UNEP), 2001).

While the fields of conservation and population ecology have acknowledged this shift in emphasis, economics as a discipline has been slow to react. Economics is the science of understanding people's behaviour and the motivations behind that behaviour. Within the sphere of species conservation, economics has been charged with investigating the incentives underlying the actions people take that lead to species loss. Given the need to develop and implement appropriate and cost-effective conservation policy (over 70 percent of all endangered species are found in developing nations (UNEP, 2001)), it is crucial for policymakers and researchers to adequately understand these incentives. In short, understanding these incentives is essential to the development of appropriate conservation policy.

Ecologists have undertaken the challenge of investigating the biological implications of species interaction. The ecological implications of modelling species in isolation rather than as part of an ecosystem are now well documented (Pimm, 1991; Begon et al., 1996; Milner-Guilland and Mace, 1998). Economists, however, have largely failed to adequately address the economic implications, which may have a profound effect on the quality of policy advice offered. Inappropriate or ill-informed policy could result in the misdirection of limited conservation funds, directing them towards areas where they are not needed or, more crucially, not being directed to areas where species extinction is imminent.

To this end, it is crucial for policymakers and researchers to recognise the significance of the single species assumption when interpreting the results of single species models. The development of a generalised multiple species framework facilitates such recognition. This thesis seeks to take up the challenge of investigating

---

[1] Although many definitions exist, biodiversity can be taken to encompass 'the variety of life forms, the ecological roles they perform, and the genetic diversity they contain' (Murphy, 1988, p.71).

the economic implications of species interaction by exploring the introduction of multiple species into the traditional bioeconomic framework.

More explicitly, the objectives of this thesis are to: Develop an analytical model to identify incentives underlying human behaviour in a multiple species framework. Develop a numerical model to test the implications arising from the analytical model. Compare the numerical multiple species model with a single species model. Finally, determine the conditions under which a single species model can be used, and those under which a multiple species model is necessary.

Following convention, the harvest levels of each species are control variables within the models. Although non-consumptive use of species may earn significant revenues (in Kenya, Elephant viewing alone has been estimated to be worth US$25 million annually (Hearne et al., 2000)), for the most part consumptive values remain the dominant sources of income. Consequently, and to retain expositional clarity, attention is restricted to these values. Recognising the role that loss of habitat plays in causing species decline (habitat loss or degradation affect 89 percent of all threatened birds, 83 percent of mammals and 91 percent of plants (IUCN, 2000)), allocation of land resources is specified as an additional control.

The remainder of this chapter explores early perceptions of extinction and briefly discusses the five periods of mass extinction in geologic history. This is followed by a discussion on measuring rates of extinction and the causes, both proximate and fundamental, of current species loss. The concept of total economic value is introduced before the global policy response to date is evaluated.

Chapter 2 reviews the relevant literature, beginning with the works of the 'Classical' economists, before turning to early developments in the field of ecological modelling. The seminal works surrounding the economics of resource exploitation are discussed, followed by a review of the development of the field of ecological economics as a sub-discipline. Extinction modelling literature is then introduced, and the chapter concludes with an examination of the fundamental models upon which the models presented in this thesis are based. Beginning with Clark's seminal (1973) model of a sole-owner fishery, attention is then focused on Clark's later model (1990), which explicitly considers the possibility of the existence of a multiple species fishery. The final model presented is Swanson (1994), who seeks to bring the modelling literature 'onshore' through the inclusion of term's representing the additional resources required for a terrestrial (as compared to a marine) species survival.

A multiple species framework is introduced in Chapter 3, combining both ecological and economic theories of species interaction. The seminal works of Lotka (1925) and Volterra (1926) are used to illustrate the ecological rationale behind a multiple species framework, while production literature, in particular the theory of joint production, forms the basis of our economic approach to the model. The analytical multiple species model is developed and comparisons are drawn between the single and multiple species results, paying particular attention to the potential consequences of misapplying a single species model to a multiple species situation. Because a multiple species model is likely to be sensitive to the relationships of included species, three cases of species interaction are considered: ecological independence, interspecific competition and predator-prey.

In Chapter 4 functional forms are specified, parameters estimated and the model solved numerically. Species independence is illustrated using the African Elephant *(Loxodonta africana)* and the White Rhinoceros. The African Lion *(Panthera leo)* and the Blue Wildebeest *(Connochaetes taurinus)* serve as examples of predator-prey interaction, while the Impala *(Aepyceros melampus)* and Greater Kudu *(Trageelaphus scriptus)* illustrate the case of interspecific competition. The numerical results serve to enhance the generalised analysis. Furthermore, the numerical application allows the model to be tested against observable 'real world' phenomena.

Finally, Chapter 5 provides a brief summary, discusses conclusions drawn from the analytical and numerical analysis of the model, notes weaknesses and shortcomings of the approach taken, and suggests areas for further research.

1.2 The Decline of Species

1.2.1 Five Extinctions

Although the phenomenon of species extinction is now an accepted fact, this has not always been the case. Species extinction was for a long time considered impossible. The ancient Greek concept of plenitude, or completeness of the natural world, implies that no organism that ever existed on the Earth could ultimately disappear from its surface because their final extinction would leave an unbridgeable gap in the 'Great Chain of Being'. Eighteenth century naturalists knew, of course, that a wide variety of fossils had no counterparts among living organisms, but this apparent anomaly was commonly explained by an as yet inadequate knowledge of life on the Earth. It appeared reasonable to assume that the missing species could still be found alive somewhere further afield. It was only after Cuvier (1799) first described the fossils of Mammoths that species extinction was established as a fact. It was hard to believe that such large and prominent mammals could roam the Earth without ever being observed by travellers, yet the concept of plenitude could still be reconciled with the fact of species extinction by assuming, as in fact Lamarck (1809) did, that man is the sole agent responsible for species extinction (Hoffman, 1989).

However, it became undeniable in the early nineteenth century that species extinction had indeed taken place in the geological past (Hoffman, 1989). In more recent times palaeontologists, through the study of fossil records dating back some 600 million years, have concluded that the process of extinction appears to have been ongoing. Certain episodes stand out as so-called 'mass extinctions'. A mass extinction can be defined as a period of substantial biodiversity losses that are global in extent, taxonomically broad, and rapid relative to the average duration of the taxa involved (Jablonski, 1986). Historically, five mass extinctions have been distinguished: the Late Ordovician, the Late Devonian, the End Permian, the End Triassic and the End Cretaceous (May et al., 1995), the latter of which has generated the most public interest, primarily due to the fate of the Dinosaurs. The nature and cause of the End Cretaceous event remains the focus of intense debate between those who suggest that the event occurred over a matter of months as a result of an asteroid impact and those who favour a longer duration. Some evidence supports both hypotheses, although the former is more popular (Garland, 1989).

1.2.2 The Sixth Extinction?

The Earth appears to be entering an era of extinction that may rival or even surpass that which occurred at the end of the Cretaceous period. Some estimates suggest the Earth is currently losing 27,000 species per year, representing a rate of extinction approaching 10,000 times greater than would exist under 'normal' circumstances (May et al., 1995). This period of extinction has been labelled the 'sixth wave'; it is comparable to the big five mass extinctions, with one important distinction: for the first time in geologic history, a major extinction episode is being caused by the actions of a single species – *Homo sapiens* (Ehrlich, 1986).

The sixth wave can be broken into two discrete phases. The first began at the very end of the Pleistocene, shortly after *Homo sapiens* evolved out of Africa and modern humans began migrating and spreading throughout the world. The fossil record suggests more than half of the large mammals of the Americas disappeared in a wave of extinction at this period. Although climate change and secondary ecological effects are among the suggested explanations, evidence strongly favours human predation as the most likely cause (Alroy, 2001). Phase two of the sixth extinction began about 10,000 years ago with the invention of agriculture. Perhaps the single most profound ecological change in the history of life, agriculture meant that humans were no longer restricted by the ecosystem's carrying capacity, and so began to overpopulate (Eldredge, 1998).

Few scientists who study the loss of biodiversity doubt that we are facing another mass extinction. There is difficulty, however, in establishing the rate at which these extinctions occur. Estimating rates of extinction, whether they are anthropocentric in origin or naturally occurring 'background' extinctions, is the focus of much effort and regarded as crucial for the development of appropriate policy responses.

The fundamental barrier to making precise estimates of the number of species being extinguished is that we do not know the number of species originally present (Wilson, 1988). Three different approaches exist to estimating likely future rates of extinction. The first, and by far the most familiar, uses species-area relations in combination with current or projected rates of habitat destruction, typically tropical deforestation (for reviews of such projections, see Whitmore and Sayer, 1992). The second method, first devised by Smith et al. (1993), provides an estimate based on the current rate at which species in better studied groups are 'climbing the ladder' of the IUCN's categories of threat from 'vulnerable' to 'endangered' to 'probably extinct' to certified extinction. The third method, first presented by Mace (1995), uses the estimated probabilities of extinction as functions of time. While each method has its relative merits and shortcomings (for a full review, see May et al., 1995), their results are surprisingly similar; that is, they all suggest a rate of extinction of between 100 and 1,000 times greater than 'normal', with most estimates approaching the latter figure (May et al., 1995).

Counter to the figures given above is a new argument of whom a principle proponent is Bjorn Lomborg. In his work *The Skeptical Environmentalist* (2001), Lomborg asserts that claims of massive species extinction do not equate with the available evidence. Lomborg points out that the rate at which species have become extinct has fluctuated over the Earth's history, and the number of species has generally increased over time. In fact, never before have there been so many species as there are now. On the method of using species-area relations in combination with rates of deforestation to calculate species loss, Lomborg notes that the correlation between the number of species and area, formulated by the biologist E.O. Wilson in the 1960s and Wilson's 'rule of thumb' - *if the area is reduced by 90 percent, then the number of species will be halved* - was developed in the context of island habitats (Mann, 1991; Simberloff, 1992). He questions the validity of extrapolating these results across large and diverse types of habitat, observing:

> If islands get smaller, there is nowhere to escape. If on the other hand, one tract of rainforest is cut down, many animals and plants can go on living in the surrounding areas.
>
> (Lomborg, 2001, p.253)

The Skeptical Environmentalist has provoked a storm of controversy; *Scientific American* devotes eleven pages to a series of articles criticising the work (Rennie et al., 2002). Scientists have reacted angrily to his suggestion that they have purposely exaggerated the true extent of environmental problems. Thomas Lovejoy, the chief biodiversity adviser to the president of the World Bank, in his review of Lomborg's chapter 'Biodiversity' remarks:

> …Lomborg seems quite ignorant of how environmental science proceeds: researchers identify a potential problem, scientific examination tests the various hypotheses…researchers suggest remedial policies - and *then* the situation improves. By choosing to highlight the initial step and skip to the outcome, he implies incorrectly that all environmentalists do is *exaggerate*. The point is that things improve *because* of the efforts of environmentalists to flag a particular problem, investigate it and suggest policies to remedy it.
>
> (Lovejoy, 2002, p.69)

Criticism notwithstanding (much of which seems directed towards Lomborg personally, rather than towards his thesis), there appears to be merit in his arguments, and the true extent of species loss most probably lies somewhere between the two extremes.

In addition to establishing the current rate of extinction, much attention has been given to identifying the cause. There is a general agreement that human activity is the principal driving force of species loss.[2] This force can be distinguished in terms of proximate (direct) and underlying (fundamental) causes.

The Global Biodiversity Assessment Group identifies three proximate causes of species extinction. These are, in order of importance, loss of habitat, the introduction of non-native species, and over-harvesting. The underlying cause is more complex and refers to the economic, social and cultural factors that lie behind the activities that lead to species loss (Barbier et al., 1994).

The most prevalent cause of extinction, and one which policy initiatives have in the large part failed to address, is loss of habitat. No organisms occur in all habitats, and most have quite narrow requirements, so it is inevitable that when habitats are destroyed, populations and eventually species become extinct. Determining the overall rate of habitat loss with precision is very difficult. Comprehensive numbers on total destruction of habitats such as clear-cutting of forests, ploughing of grasslands and draining of wetlands are not available. Nonetheless, the figures that are available give a feel for how extensive the destruction has been. Percentages of total forest area that has been lost are available for a sample of 40 African nations and range from 30 percent in Zambia to 91 percent in The Gambia, with an average of 68 percent. Losses in 14 Asian nations (excluding China) range from 34 percent to 96 percent with an average of 69 percent. India has lost some 78 percent of all its forests (World Resources Institute (WRI), 1990). Further to these losses, a significant number of forests that have survived thus far are threatened today. The WRI assessment found that 39 percent of the Earth's remaining frontier forests are endangered by human activities. Despite a large body of research devoted to analysing the sustainability of developed nations' use of forest resources (see, for example, van Kooten et al., 1999), the primary use of the world's wood is not as building materials or paper, but as fuel, with 63 percent of all wood harvested burned as fuel (WRI, 2000).

---

[2] Even Lomborg acknowledges '...mankind has long been a major cause of extinction' (2001, p.251).

Forest is not the only habitat to be disrupted; the extent of total habitat destruction varies among habitat types and regions. In the United States, virtually all of the natural grasslands have been lost. Many Western nations including Germany, the United States and New Zealand have lost substantial areas of wetland. About 75 percent of the coastal mangrove wetlands of India, Pakistan and Thailand are gone (Brown, 1992; WRI, 1992).

In addition to total destruction, the degradation of habitat quality, especially that of freshwater habitats where 12 percent of all animal species live, is also a major cause of species loss. Major disruptions to freshwater habitat include the building of dams and the excessive use of rivers for irrigation (Revenga et al., 2001). Measuring habitat degradation is significantly more difficult.

Competition from non-native plant and animal species represents a growing threat to natural ecosystems. Exotic 'invaders' currently threaten some 20 percent of vertebrate species. The growth of world trade has seen the dramatic increase of this 'bio-invasion', and it is now considered to be the second greatest threat to species (WRI, 2000).

A good example of multiple threats to a single species posed by a variety of introduced organisms can be found in the case of the Brown Kiwi (*Apteryx mantelli*). Introduced predators are the main threat. About 50 percent of Kiwi eggs fail to hatch; many are eaten by Possums *(Didelphis marsupialis)*, Stoats (*Mustela erminea*) and Ferrets *(Mustela putorius furo*). Of the eggs that do hatch, around 95 percent of chicks are eaten by Stoats and Cats (*Felis catus*) before they are six months old. Older birds can defend themselves from these predators, but they remain vulnerable to Dogs *(Canis familiaris)* and Ferrets (Kiwi Recovery Programme, 2002).

The overexploitation of resource stocks is often thought to be the main cause of species extinction. While this was a contributory factor in the decline of a large number of species during early periods of human expansion, even abundant species can become extinct in a relatively short period of time if exploitation is excessive; commercial exploitation is seldom, if ever, the sole cause of extinction.

The Passenger Pigeon (*Ectopistes migratorius*) showed a spectacular decline in number from several billion in 1810 to around 200 million in 1870, to one captive female only 40 years later, and finally extinction in 1914. This is frequently used as a classic example of overkill leading to extinction (King, 1987). However, Bucher (1992) presents a convincing counter-argument. He contends that the Passenger Pigeon became extinct primarily as a result of forest destruction and fragmentation, particularly in its northern breeding grounds. Habitat destruction, coupled with an absence of social cooperation among the birds in food finding at low densities, would have been enough to lead to their extinction even without human exploitation (du Plessis, 2000).

Nonetheless, many current examples of species being threatened by over-harvesting persist. In addition to the well-documented examples of species being harvested for their high value by-products such as ivory and hides, many endangered species, especially those in developing nations, are harvested for food. According to the IUCN, the practice of hunting wildlife for food affects 30 endangered species including Gorillas, Chimpanzees and Monkeys, posing a significant threat to their existence (Hearn, 2001).

1.3 The Economics of Species Loss

1.3.1 The Fundamental Forces

In attempting to address the global problem of species loss, it is necessary to look beyond the proximate causes and come to grips with the fundamental forces that lead humans to behave in such a way that leads to the endangerment and possible extinction of other species.

Pearce and Moran (1994) categorise the fundamental causes of species loss into three areas. First and most crucially, human population growth leads to increasing amounts of the base resource (land), being converted into non-conservation uses. Second, market failure, which is the failure to create markets or modify existing markets for species so that they fail to secure economic value to compete with alternative uses of the base resource upon which they depend for survival. Third, intervention failures, meaning government-provided incentives such as subsidies to farmers, which simply exaggerate the rate of return to the alternative use of land.

The notion of market failure leading to the loss of species is given comprehensive treatment by Panayotou (1992). Addressing the wider concern of environmental degradation, Panayotou identifies a number of market failures affecting the use and management of natural resources. Those most significant to the issue of species loss are as follows: ill defined or absent property rights, high transaction costs, myopic planning, and irreversibility.

A fundamental condition for the efficient operation of markets is that there exist well-defined, exclusive, secure, transferable and enforceable property rights over all resources, goods and services. Property rights are a precondition to the efficient use, trade, investment, conservation and management of natural resources. In the absence of such rights, an individual is unlikely to invest in the conservation or management of the resource, as securing a return to the investment is at best uncertain, and in many cases impossible. Markets emerge to make possible beneficial exchanges or trade between parties with different resource endowments and different preferences. Absence of well-defined property rights prevents markets from emerging as there is no owner who can demand a price, and in their absence deny access; moreover, there is no buyer who would be willing to pay a price as long as they have free access to the resource elsewhere (Panayotou, 1992).

Clearly, for the case of most endangered species, with the exception of those inside reserves or zoos, property rights are clearly lacking. In fact, many are characterised (in particular marine species) by an open-access regime where those wishing to obtain access are free to do so.

Unfortunately, the establishment of well-defined property rights will not necessarily bring markets into existence if transaction costs are very high. A good illustration of this is the problems wildlife managers in large African game reserves face with poachers. Here the property rights are clear, but the enforcement costs of those rights are prohibitive. A further example can be seen in New Zealand, which has the exclusive rights to a large marine fishery, but insufficient resources to prevent others from encroaching on those rights.

Natural resource conservation and sustainable development ultimately involve a sacrifice of present consumption for the promise of future benefits. Because of time preference, such an exchange appears unattractive unless today's sacrifice yields greater benefits tomorrow. Future benefits are discounted, and the more heavily they are discounted the less attractive they are; a high discount rate may discourage conservation altogether. If the market rate of interest accurately reflects the society's rate of time preference, then (except for the issue of irreversibility) an optimal outcome could result. However, in developing nations particularly, a short and uncertain lifespan, coupled with a 'hand to mouth' subsistence standard of living, leads people to adopt myopic time horizons and discount rates that result in short-sighted decisions in pursuit of survival, or quick profits at the expense of long-term sustainable benefits (Panayotou, 1992).

Central to this idea is the notion of inter-generational equity. It is clear that any change in biodiversity has implications not just for the present, but also for future generations. Although the preferences of future generations are unknown to us today, it would seem reasonable to assume that they will also attribute value to natural resources. Unfortunately, the choices we are making today may actually mean less biodiversity available for future generations. There is vigorous debate over the role inter-generational equity should play in conservation decisions. Those who value inter-generational concerns highly advocate a zero discount rate for projects with long-term benefit streams.

While many market decisions are made on the assumption that they can be reversed if the outcome is not as desirable as first supposed, this assumption does not hold true in decisions involving natural resources. Once a species becomes extinct, there is no turning back; in contrast, choosing to conserve a species preserves our options. Clearly there is a social value or shadow price for the preservation of options, although it is difficult to estimate.

There are reasons to suggest this shadow price may be high. Technical change expands our ability to produce ordinary goods, but does little to improve our ability to produce natural resources (with the possible exception of increasing extraction efficiency). Furthermore, as a nation's wealth grows, consumer's preferences tend to shift in favour of environmental services relative to ordinary goods (Krutilla, 1967; Panayotou, 1992).

Swanson (1994; 1994a) considers species loss to be a result of a failing to include particular species within the 'global portfolio' of assets. Further discussion of Swanson's thesis can be found in the following chapter.

1.3.2 The Value of Species

Given that species are becoming extinct at rates far greater than 'normal' and given that human activity is by far the most likely cause of these extinctions, it is not surprising that a considerable (but insufficient) amount of the world's resources are currently being devoted to conservation effort. Why are we attempting to save species? The answer to that question at the most fundamental level is because we derive value from their continued existence.

The economic value of something is measured by the willingness of many individuals to pay for it. In turn, this willingness to pay reflects individuals' preferences for the good in question. Valuation is therefore based on preferences held by people; it is anthropocentric in origin. The resulting valuations are in monetary terms because of the way in which preferences are revealed, i.e. by asking people what they are willing to pay, or inferring their willingness to pay through other means. Moreover, the use of money as a measure of value permits comparison.

Many people believe that biological resources possess intrinsic value; that is, they are of value in themselves, independent of humankind. Although it is important to recognise from the outset that both economic and intrinsic value exist, it is the former, in particular Total Economic Value (TEV), that I focus on here. This choice comes from recognising that it is economic value that has the most bearing upon the ultimate fate of a species.

The economic value of biological resources can be broken down into a set of component parts. In a conservation context, TEV can be seen as a measure of the benefit to humankind (given a set of individuals' preferences) of the continued existence of a species or ecosystem. TEV comprises both use and non-use values. A use value is a value arising from an actual use made of a given resource and can be divided into direct use values, indirect use values and option values.

Direct use values are fairly straightforward in concept, but not necessarily easy to measure. They refer to activities such as fishing and timber extraction or the use of plants for pharmaceutical research. Indirect use values correspond to the ecologist's concept of 'ecological functions', and might include such things as a forest's function as a carbon sink This value is stressed in the work *Paradise Lost? The Ecological Economics of Biodiversity* (Barbier et al., 1994). The authors point out that ecological functions are uncertain, and may support or protect economic activity and property far removed from the ecosystem generating the function, thus generating a value that may be significant, but is often intangible. Option values are those amounts that an individual would be willing to pay to conserve a natural asset for future use; that is, no use is made of it now, but use may be made of it in the future.

Non-use values relate to valuations of the resource unrelated to either current or potential future use. Existence value is based upon the observation that many people reveal a willingness to pay for the existence of natural resources through charities such as the World Wildlife Fund for Nature, without actually taking part (or intending to take part) in the direct use of the resource being conserved. To some extent, this willingness to pay may represent 'vicarious' consumption, such as consumption of wildlife documentaries and magazines, but studies suggest that this is a weak explanation for existence value. Empirical measures of existence values suggest that existence value can be a substantial component of TEV. Furthermore, it has been demonstrated that in many cases some existence value must be appropriated to the resource in order for extinction to be avoided (Pearce, 1993; Pearce and Moran, 1994; Moran and Pearce, 1997; Alexander, 2000).

1.3.3 The Global Policy Response

Response to the endangerment and loss of species has encompassed the efforts and resources of a wide range of groups of people. Governments, non-government organisations, businesses and individuals have all sought to make their contribution to conservation efforts. I will not attempt to provide an exhaustive review of the various policy efforts, choosing instead to focus on the international response.

An early attempt to use international legislation to promote wildlife conservation was the 1911 Fur Seal Convention, designed to deal with the problem of over-exploitation of the Fur Seals of the Pribilof Islands off the coast of Alaska. Such moves have led to several other conventions, including the International Convention of the Regulation of Whaling in 1946, still in place in a modified form today (International Whaling Commission, 2002).

During the 1950s, conservationists began to focus on the escalating international trade in both live animals and their products. At first this attention was narrowly focused on a small range of species including Spotted Cats (traded for their furs), Primates (used in medical research) and Crocodiles (killed for their skins). In time the concern widened. By 1960 there was sufficient international impetus for the

IUCN at its General Assembly to urge governments to take action. The IUCN's next General Assembly in 1963 passed a resolution calling for an international convention to address the issue. This was followed by a first draft of such a convention in 1964. The IUCN General Assembly in 1969 and the United Nations Conference on the Human Environment in Stockholm in 1972 provided the final motivation, and The Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) was born (Huxley, 2000).

Originally signed following a three-week conference in Washington DC. in 1973, CITES came into force two years later. The aim of the convention was to save wild species from extinction by means of the regulation and restriction of the international trade in wildlife. The main thrust of the convention was the establishment of a set of import, export and re-export controls on species listed in the three appendices, the most stringent of which is Appendix I, which includes "...all species threatened with extinction which are or may be affected by trade" and stipulates "Trade in specimens of these species must be subject to particularly strict regulation in order not to endanger further their survival and must only be authorized in exceptional circumstances" (Text of the Convention, Article II: Fundamental Principles, 2002).

For most of its existence CITES has been the major tool possessed by the international community for preventing the loss of species, and high expectations have been placed on it. At the time there was very little knowledge of the nature and magnitude of international trade in specimens of wild species. Nevertheless, there was a strong feeling that international trade was a significant cause of species decline.

CITES has proven to be controversial since its inception, and 27 years later the treaty is still surrounded by controversy. Four developments over the last quarter of a century are important. Most importantly, there have been improvements in our understanding of the threats to wild species. The convention is founded on the assumption that the international trade in wildlife is an important threat to their continued existence. Indeed, it is the only threat it addresses. Part of the weakness of CITES is that it has not always been successful in enforcing its bans and regulations. A much more serious difficulty is that for many species international trade is not the primary threat. It is now recognised that other processes, in particular the loss of habitat, the introduction of exotic species, and the bush-meat trade, are much more significant; thus for many species the CITES remedy will be quite inappropriate (Hutton and Dickson, 2000; Martin, 2000).

Indeed, there is an argument that the policies offered by the convention have actually exacerbated the problem. This argument asserts that for investment in a species' conservation to take place, the species must be able to generate a monetary return, sufficient to offset the opportunity cost of using its habitat (and other base resources) in an alternative way. Imposition of trade restrictions, through cutting off a potential source of revenue, effectively undermines the ability of the species to generate a return, making it a less attractive 'investment' option (Swanson, 1994; Bulte and van Kooten, 1996).

A second development has been that developing nations have become more forceful in putting forward their own case. While the conservationists of developed nations largely created the original convention, southern African nations in particular have emphasised the need for conservation policies to provide tangible benefits to those who live closest to the wildlife. This view has been criticised by those who see it as providing a license for the unregulated exploitation of wildlife.

The third development has been an increasing emphasis on the social dimension of conservation. As the fate of wildlife is so closely entwined with changes in human society, a policy for wildlife is simultaneously a policy for society, raising questions of justice and equity within the distributions of the costs and benefits of wildlife. The growing popularity of the notion of sustainable development, with its acknowledgement of a linkage between environment and social concerns, has served to fuel this debate (Hutton and Dickson, 2000).

A final development was the signing of the CBD. Signed at the United Nations Conference on Environment and Development in 1992, the CBD, like CITES, is concerned with the loss of species, but it is a more comprehensive convention, and one that takes into account the lessons of recent years. It does not focus on just one threat to wildlife, and it does not offer just one remedy. The convention has three goals: the conservation of biodiversity, the sustainable use of the components of biodiversity, and the sharing of the benefits arising from the use of genetic resources in a fair and equitable way (UNEP, 2001).

There is a consensus that CITES needs to move closer to the CBD. In light of the fact that the goals of the two coincide and that comparison between the two favours the latter, there is a strong case for subsuming CITES within the CBD. It should not be too surprising that the CBD should provide a better framework for conservation. It has had the advantage of twenty years of progress in conservation thinking and practice. The CBD possesses all the ingredients for a holistic approach to conservation and sustainable use. It is a force for the decentralisation and devolution of responsibilities to local communities, both in the developed and developing world. Its recognition of the need for incentives for people and the placing of economic value on wild resources puts it in the category of 'conservation with a human face' as opposed to the 'command and control' regime of CITES. Although at this point in time CITES remains independent, the eventual merging of the two seems inevitable (Bell, 1987; Martin, 2000).

CHAPTER II

LITERATURE REVIEW

2.1 An Overview

2.1.1 The Classical Economists (and beyond)

Although the emergence of natural resource economics as a distinct sub-discipline has been a relatively recent event, concern with natural resource and environmental issues within the field can be traced back as far as the 'Classical' economists of the eighteenth and nineteenth centuries. The birth of economics as a discipline is traditionally associated with the work of Adam Smith in the late eighteenth century. In his major work, *An Inquiry into the Nature and Causes of the Wealth of Nations* (1776), Smith develops the perception that the 'value' of nature is merely instrumental; that is, valuable only if it serves human wants. This view remains a central tenet of mainstream economics, as it exists today.

> The earth furnishes the means of wealth; but wealth cannot have any existence, unless through industry and labour which modifies, divides, connects, and combines the various production of the soil, so as to render them fit for human consumption.
>
> (Smith, 1776)

Although Smith was writing at a time when the availability of natural resources was not, in general, a constraint of the economy, it was an issue soon to arise. At the beginning of the nineteenth century, economic thought was preoccupied with the question of what factors determined a nation's rate of economic growth and therefore its standard of living. A key concern was the limitations that a potentially fixed supply of natural resources, in particular land, may have in the long-term. Perhaps the most notable (yet misguided) attempt to address this issue belongs to Thomas Malthus. Although by no means the first writer to speculate on demographic problems, Malthus was the first to succeed in devising a theory of population growth. In *An Essay on the Principle of Population* (1798), Malthus theorised that a subsistence level existence was the most likely long-run outcome of human development. He contended that continued population growth, coupled with diminishing returns to agriculture, implied a tendency for output per capita to fall over time and that this would continue until standards of living were so low that population growth was halted. Dismal as his thesis was, Malthus received widespread popular support. In fact, the writings of Malthus had a great deal of influence on Charles Darwin and led to Darwin's concept of 'survival of the fittest' as a central theme in the theory of natural selection (Pielou, 1974; Blaug, 1997; Perman et al., 1999).

David Ricardo more formally addressed the notion that human development, due to the limited supply of natural resources, would inevitably result in a subsistence level existence. In his *Principles of Political Economy and Taxation* (1817), Ricardo pointed towards the need, in the face of population growth, to increase agricultural output. This, he asserts, could only be achieved by either cultivating a given piece of land more intensively or by bringing previously uncultivated land into use. In either case, returns to the land input were taken to be diminishing, with the consequent return to subsistence in the long-run (Perman et al., 1999).

Some 50 years later W. Stanley Jevons (1865) spread the concern to mineral resources by observing the physical limits of coal deposits in England and predicting the end of the industrial revolution as a result. This conclusion was supported by Leonard Courtney (1897) who, upon measuring a decline in England's industrial growth, declared that Jevons was correct (Fisher and Peterson, 1977).

John Stuart Mill (1857) was among the first classical economists to recognise that the growth of knowledge and technical progress could provide a counter-force to the onset of diminishing returns. He also pointed to the role of colonial expansion in providing an additional source of natural resources. Although Mill retained the view that development would inevitably lead to a stationary state, he was of the opinion that such a state could occur at a comparatively high standard of living.

Utilitarianism (1863) represents another of Mill's contributions to natural resource economics. Although utilitarianism[3] originated in the writings of David Hume (1739; 1751) and Jeremy Bentham (1789), it found its most complete expression in the work of Mill (Perman et al., 1999). Equally visionary in retrospect, however, was Mill's formal adoption of a broader view of the role of natural resources in human welfare. Not only did he consider the agricultural and extractive value of land he also

---

[3] A consequentialist (where the consequences or outcomes of an action determine the moral worth of the action) philosophy which remains the fundamental ethical foundation of the field (Perman et al., 1999).

acknowledged it as a source of amenity value, a value he envisaged increasing, as standards of living rose. This view is clearly expounded in the following passage:

> ...nor is there much satisfaction in contemplating the world with nothing left to the spontaneous activity of nature: with every rood of land brought into cultivation, which is capable of growing food for human beings; every flowery waste or natural pasture ploughed up, all quadrupeds or birds which are not domesticated for man's use exterminated as his rivals for food, every hedgerow or superfluous tree rooted out, and scarcely a place left where a wild shrub or flower could grow without being eradicated as a weed in the name of improved agriculture. If the earth must lose that great portion of its pleasantness which it owes to things that the unlimited increase of wealth and population would extirpate from it, for the mere purpose of enabling it to support a larger, but not a happier or better population, I sincerely hope, for the sake of posterity, that they will be content to be stationary long before necessity compels them to it.
>
> (Mill, 1857, Book IV)

2.1.2 Early Ecological Modelling

The effects of Malthus' predictions were widespread. Population modelling owes much to his work. Malthus' dire predictions stimulated an early mathematical formulation of the principles of population growth and limitation by Belgian Pierre Francois Verhulst (1838). Verhulst's logistic growth model remains a fundamental hypothesis in ecology, forming the basis of population growth functions adopted in much of the subsequent literature. Among those to use Verhulst's equation, and the first to explicitly consider the modelling of species interdependence, were Lotka (1925) and Volterra (1926). These authors independently (Lotka in the United States and Volterra in Italy) derived equations of two interacting populations, considering where both species were competitors and where one species was a predator and the other prey. Commonly called the Lotka-Volterra equations,[4] these remain the initial points of reference when considering species interdependence.

One of the first and most important tests of these equations was performed in 1932 by a Russian microbiologist, who studied competition between two species of yeast, *Saccharomyces* and *Schizosaccharomyces* (Gause, 1932). Alone, both species grew according to the logistic curve. However, where the two species grew together,

---

[4] Although some authors refer to the case of interspecific competition as Gause's model.

population densities were lower than under single species conditions. Gause (1934) went on to provide the first clear example of extinction caused by the presence of a competitive species. Gause found that when the two species *Paramecium aurelia* and *Paramecium caudatum* were placed in the same culture, *P. aurelia* always approached a carrying capacity (albeit a lower one than when cultivated alone), whereas *P. caudatum* eventually died out. Gause concluded that *P. caudatum* lost out as a result of interspecific competition. These results led Gause to postulate that no two species can coexist indefinitely on the same resource, a concept that has come to be known as the competitive exclusion principle, or Gause's Law (Krohne, 2001). In addition, Gause (1934) devised experiments to test predator-prey interactions. Using *Paramecium caudatum* as the prey and *Didinium* as the predator, Gause found predator extinction always occurred. Either the predators drove the prey to extinction, resulting in a complete loss of food resource, or in some cases the predators became extinct before the prey, and the remaining prey reached carrying capacity (McNaughton and Wolf, 1979).

2.1.3 The Economics of Resource Exploitation

Early economic models of resource exploitation concentrate not upon renewable or biological resources, but upon non-renewable resources.[5] Lewis Gray (1914) formulated the first comprehensive theory of the mine, taking a static approach; he was able to deduce properties of the time path of prices and the effects of taxes and price changes. Hotelling (1931), taking a dynamic approach to the problem, posits that a natural resource represents a capital asset to society and to its owner, much like any other form of capital. However, unlike manmade or 'physical' capital, a non-renewable resource is not reproducible; that is, the size of the stock cannot increase. As a resource deposit draws its market value from the prospect of extraction and sale, the only means a non-extracted resource deposit has to afford a current return to its owner is to appreciate in value. This, coupled with the recognition that an asset market can be in equilibrium only when all assets (of equal risk) earn the same rate of return, derived the efficiency condition, known as 'Hotelling's Rule', that an extraction program requires the net price of the resource to grow at the same rate as the discount rate. This condition remains a fundamental principle of the economics of

---

[5] Following the convention established by Ciriacy-Wantrup (1952), extractive resources are defined as renewable or non-renewable, depending on whether they exhibit economically significant rates of regeneration.

exhaustible resources (Solow, 1974). Dealing specifically with the gold supply but deriving results of greater generality, Frank Paish (1938) distinguished between extraction from existing mines and investment in new ones, arguing that uncertainty and high interest rates would accelerate the former and discourage the latter.

The literature surrounding the extraction of renewable resources has grown predominantly out of the fisheries literature. Fisheries biologist Michael Schaefer (1954; 1957), another to adopt the Verhulst logistic growth model, is generally considered the pioneer in this field. It is his model of commercial fisheries populations, where harvesting was given as a function of fishing effort and 'catchability', which forms the basis of Gordon's (1954) model of an open-access or common property fishery. Gordon demonstrates that firms enter freely and drive rents to zero when a fishery is a common property and no cooperative agreements have been reached. Each firm ignores or underestimates the diseconomies of crowding that they generate, as well as the user cost of depleting the stock of fish, that is, competitive exploitation of a fishery results in more effort and lower stocks than are optimal (Fisher and Peterson, 1977). The problem of an open-access resource being over-exploited is often referred to as the 'tragedy of the commons' after Hardin's (1968) article of the same name. Hardin uses the example of open pasture, demonstrating that if each herdsman, acting rationally, continued to add cattle to his herd as long as it remained to his benefit to do so, the end result would be a level of grazing in excess of the socially optimal level.

Central to Gordon's (1954) model and to Hardin's (1968) thesis is the issue of property rights. Clearly the case of open-access or common property is one where no individual has well-defined or enforceable property rights. Coase (1960) sought to address this in his article 'The Problem of Social Cost'. The proposition or propositions, now referred to as the Coase Theorem, was originally developed through a series of examples. A central insight in microeconomics is that free exchange tends to move resources to their highest value use, in which case the allocation of resources is said to be *Pareto Efficient*.[6] Working from this insight, Coase argues that, in the absence of transaction costs, economic efficiency will be achieved as long as property rights are fully allocated and able to be freely traded.

---

[6] An allocation is Pareto Efficient if there is no other allocation in which some individual is better off and no individual is worse off.

Using the now classic examples of bees and lighthouses, the Coase theorem sought to demonstrate that under these conditions, externalities and public goods did not automatically call for government intervention. However, as Coase acknowledges, a costless transaction serves as a logical construct, rather than something encountered in the real world.

Swanson (1994a) provides further discourse on open-access versus well-defined property rights and the implications for species conservation. Swanson notes that all terrestrial (unlike marine) resources fall within the bounds of some state's jurisdiction. Therefore, a terrestrial open-access regime is not inherent in the nature of the asset, but the consequence of societal choice. Swanson contends that the decline of the African Elephant in the 1980s was a result of 'arm's length exploitation'. Arguing that, African states could have better regulated the exploitation of this species, but chose not to, tacitly endorsing the overexploitation that inevitably resulted.

2.1.4 The Development of Ecological Economics

In addition to the field of natural resource economics, which primarily addresses the way we allocate the resources that come naturally from the Earth, are two schools of scientific research that deal with economy-environment interactions, one called *environmental economics* and the other *ecological economics*. While these two terms are largely synonymous as far as the literal meaning of the words is concerned, there nevertheless exist distinct features characterising the two approaches and setting them apart.

While environmental economics analyses the role of nature for the human economy and, thus, conceives nature as part of the overall economy (much like an additional economic sector within an input/output representation of economic activity), ecological economics studies economy-environment interactions from a point of view that stresses that the human economy is an open subsystem of a larger, closed and non-growing physical system (Daly, 1992). Another difference between the two approaches can be seen in the scientific methods employed. While environmental economics firmly rests on the methods of neoclassical economics, ecological economics is committed to methodological pluralism[7] and favours an interdisciplinary approach (Norgaard, 1985; 1989).

Kenneth Boulding's (1966) classic, *The Economics of the Coming Spaceship Earth,* sets the stage for the development of ecological economics, with its description of the transition from the 'frontier economics' of the past where growth in human welfare implied growth in material consumption to the 'spaceship economics' of the future, where growth in welfare can no longer be fuelled in this manner. Boulding characterised the contrasting views of the environment as a limitless resource, with the modern view of its essential finitude, as the difference between the 'cowboy' and 'spaceship' view of the Earth. The cowboy symbolises the view that the natural environment is an endless frontier to be conquered; in the spaceship view there is a large but closed ecosystem with finite capacities to absorb the waste products of human activity (Pearce, 1993).

Daly (1968) further elaborates this fundamental difference in vision and world-view in recasting economics as a life science – akin to biology and especially ecology, rather than a physical science such as chemistry or physics. This implies a fundamental change in the perception of the problems of resource allocation and how they should be addressed. Specifically, it implies that the focus of analysis should be shifted from marketed resources in the economic system to the biophysical basis of interdependent ecological and economic systems. He also urged a change in perception of what constitutes economic success (Costanza, et al., 1997; Perman et al., 1999).

The model established by Boulding (1966) relies on the characterisation of the Earth as a closed system with limited opportunities for exchanging materials and energy outside that system. A similar kind of approach was taken by Georgescu-Roegen (1971) in *The Entropy Law and the Economic Process*, in which he traced out the implications of the laws of thermodynamics for economic activity. Like Boulding, Georgescu-Roegen considered the economic system as embedded within a finite wider physical environment.

The theme of absolute resource scarcity, so predominant in Malthus' time, was revisited in the late 1960s. *The Limits to Growth* (Meadows et al., 1972) was

---

[7] Pluralism is the thesis that the use of multiple theoretical models in the course of scientific practice is legitimate.

published following a meeting in Rome in 1968 of a group of diverse professionals. Based on a technique known as *systems dynamics*, a large-scale computer model was constructed to simulate likely future outcomes of the world economy. Three main conclusions were reached by this study. The first suggests that within a timespan of less than 100 years, with no major change in current physical, economic, or social relationships, society will run out of the non-renewable resources on which the industrial base depends. When the resources have been depleted, a collapse of the economic system will result, manifested by massive unemployment, decreased food production, and a decline in population as the death rate soars.

The second conclusion of the study is that piecemeal approaches to solving the individual problems will not be successful. To demonstrate this point, the authors arbitrarily double their estimates of the resource base and allow the model to trace out an alternative vision based on this new higher level of resources. In this alternative vision the collapse still occurs, but this time it is caused by the excessive pollution permitted by the greater availability of resources. As its third and final conclusion, the study suggests that overshoot and collapse can be avoided only by an immediate limit on population and pollution, as well as a cessation of economic growth (Tietenberg, 1992).

Unsurprisingly, this work stimulated widespread debate and had many opponents. Among those presenting more optimistic projections were Beckerman (1974), Kahn et al., (1976) and Simon and Kahn (1984). Today there is general consensus that *The Limits to Growth* approach was overly pessimistic (Edwards-Jones et al., 2000).

This period also saw the publication of a number of books and papers concerning wilderness development. Many of these originated with Washington DC. 'think-tank' Resources for the Future, in particular the authors John Krutilla and Anthony Fisher. Although Mill (1857) had recognised the amenity value (as opposed to the extractive value) of natural resources, systematic economic analysis of alternative uses appears to begin with Krutilla's article *Conservation Reconsidered* (1967). Starting from the work of Barnett and Morse (1963), which suggests that due to advances in technology, the traditional concerns of conservation economics (the husbanding of natural resource stocks for the use of future generations) were becoming obsolete. For Krutilla, the central issue had become:

> ...the problem of providing for the present and future the amenities associated with unspoiled natural environments, for which the market fails to make adequate provision.
>
> (Krutilla, 1967, p.778)

Specifically, Krutilla is concerned with natural environments whose use for extractive purposes precludes use for other purposes and is irreversible. Initially focusing on the disparity between private and social returns to the use of environmental goods, he suggests two reasons for this divergence. First, unlike the extractive resources, the amenities may have no close substitutes; demand is therefore not perfectly elastic, and the resource owner would have to perfectly discriminate in pricing to capture the full value of the preserved environment. Second, many of the non-extractive uses of the site are public in nature. The private owner has, for example, no way to appropriate the option value associated with preservation. Moving to dynamic considerations, Krutilla (1967) suggests that technology, unlike a site's extractive resource, cannot provide substitutes for a site's amenity services. Therefore, as technology progresses, the relative value of the former falls. In addition, Krutilla considered fashion to be changing in favour of retaining the amenity. For both reasons, changes in technology and in fashion, natural environments represent assets of appreciating value. This, coupled with the irreversibility of the destruction of natural environments, is problematic, as it would suggest current provision of such environments would be less than future generations would desire (Fisher and Peterson, 1976).

In addition to concern surrounding the loss of natural environments was a heightened public awareness of the impact of human activities, in particular the impact of harvesting, has on a growing list of endangered species.

2.1.5 The Modelling of Extinction

Although the bioeconomic literature has recognised the possibility of harvesting a species to extinction (Smith, 1969; Bachmura, 1971; Gould, 1972), the most extensive analysis is by Clark (1973; 1976; 1990). Working from Gordon (1954), Clark (1973) develops a model to analyse the decision-making of a sole owner seeking to maximise the present value of his harvests. He identifies the conditions under which the owner has an economic incentive to harvest the species to extinction. Clark identifies three conditions that would make such a choice optimal.[8] These are 1) open-access to the resource; 2) price-to-cost ratio of harvesting the resource greater than one; and 3) low growth rate of the resource relative to the social discount rate.

If either the first condition or the last two conditions are met, then resource extinction can occur. As in Gordon's (1954) model, open-access to all harvesters results in overexploitation of the resource and driving of economic rents to zero. If the growth rate of the resource is less than the return available from other assets and the price of the harvested species is greater than the cost of harvesting, there is an incentive to convert the biological asset into one earning the higher rate of return.

Many extensions have been made to Clark's original model. Clark (1976) extends the model significantly by analysing the case of endogenous prices, and including the age structure of fish populations as well as analysing the possibility of periodic fishing, rather than sustained fishing as in the original. Clark et al. (1979) study the effects of irreversible capital investment, concluding a short-run situation exists during which a fishery faces an overcapacity of harvesting resources, before leading to a long-run equilibrium situation of optimum sustainable yield. Berck (1979) considers the possibility that firms may be better off leaving their boats in port when the fish density gets too low. Demonstrating that, this short-run shutdown is enough to save a population from extinction if the fish left when the shutdown occurs are numerous enough to sustain the species.

Although others had applied versions of the model to resources other than fish, Hammack and Brown (1974) develop optimal management schemes for migratory Waterfowl; Smith (1975) uses the model to explain prehistoric animal extinction; and Beddington et al. (1975) calculate the optimal harvesting rates for Red Deer *(Cervus elaphus)*. It was not until Swanson (1994) sought to develop a generalised framework for the analysis of species extinction and biodiversity loss that the literature truly moved 'on-shore'. Swanson (1994), recognising that, unlike marine species, terrestrial species compete with humans for the use of land resources, includes land resources as an additional control variable. Using the African Elephant as an

---

[8] One must carefully consider the meaning of *optimal* in this case. Within the bioeconomic framework, the 'optimal' outcome is a reflection of incentives faced by resource owners, not necessarily an indication of the best outcome for society as a whole.

example, Swanson is able to draw policy conclusions that differ markedly from those offered by Clark's (1973) analysis.

Following Swanson's lead, many authors have attempted to construct bioeconomic models of the world's endangered terrestrial species. The African Elephant seems to have captured the most attention, in part due to their charismatic nature, and in part due to the ongoing debate surrounding the CITES trade ban. Bulte and van Kooten (1996; 1999; 1999a) have produced a significant body of work addressing this issue. *A Note on Ivory Trade and Elephant Conservation* (1996), using the range-state of Kenya as a case study, demonstrates that the ban's effect on Elephant populations is ambiguous. Depending on the discount rate, the trade ban can either increase or decrease optimal population size. If the decision-maker's discount rate exceeds a certain threshold, the optimum stock of Elephants is greater with a trade ban. Furthermore, as the rate of time preference (discount rate) is likely to decline over time, as the economy and per-capita income grows, the authors conclude:

> ...it is necessary to frequently reassess instruments implemented in the past. The same instrument (e.g. a trade ban) that worked well yesterday could be detrimental to Elephant conservation at a future date.
>
> (Bulte and van Kooten, 1996, p.441)

As the field of bioeconomic modelling has grown, so too have the range of application and level of complexity. Many extensions have been proposed redefining the potential returns accruing to resource owners. Clark's (1973) original considered only returns from harvesting the species, and although Swanson mentions a 'flow of social benefits' (1994, p.815), he does not expand on this concept. Clearly, in the presence of a trade ban, the return from harvest would be low. An author who acknowledges tourism values, although does not explicitly model them, is Anders Skonhoft (1998), who seeks to analyse the conflict between wildlife conservation and the effect it has on local people. His model consists of two agents: a park agency managing a national park and a group of agropastoralists living in the vicinity of the park. He demonstrates that for the local people to benefit from wildlife conservation they must receive a profit share from tourist activity in addition to an allowable hunting quota.

Again considering the harvest and non-harvest case, Skonhoft (1999) analyses the optimal management of species when land use costs, non-consumptive benefits and nuisance costs are taken into account. Skonhoft concludes, in each case, that an increase in profitability of alternative land use activities (such as farming) will lead to a long-run loss of habitat and consequently animal numbers. Bulte and van Kooten (1996; 1999; 1999a) introduce potential returns from wildlife tourism in addition to revenues from harvest for the case of the African Elephant.

Alexander (2000) developed a model, using the African Elephant as an example, to explicitly consider the role non-consumptive values play in wildlife conservation. Alexander demonstrates the need to consider both consumptive and non-consumptive values in exploring the potential of an endangered species to provide an adequate return to successfully compete for land resources. He concludes that in addition to tourism revenue:

> ...it is critical to the survival of the species that a way is found to appropriate the non-consumptive, non-use existence value held primarily by residents of developed nations...models and policies that fail to consider existence values are likely to consistently undervalue the wildlife resource and suggest inappropriately low optimal population levels.
>
> (Alexander, 2000, p.267)

Further extensions include Bulte and van Kooten (1999b), who analyse the implications of metapopulation (interconnected sub-populations of a single species) dynamics for optimal harvesting. These authors (2001) also address the issue of population viability for the harvesting and conservation of species with existing low populations, in particular analysing the role of minimum viable populations, below which a species is driven to extinction.

2.1.6 Multiple Species Modelling

A notable feature of the aforementioned models is their single species focus. Although the ecological framework for modelling multiple species has been in place since the work of Lotka (1925) and Volterra (1926), and ecologists frequently analyse the behaviour of multiple species systems (Klausmeiser, 1998; Mills and Shenk, 1992), with rare exceptions economists have confined their studies to the analysis of a single species. Indeed, there exist very few bioeconomic models of species interactions.

Clark (1976; 1990) provides the framework for the case of a multiple species fishery, using 'real world' examples to illustrate; however, he does not attempt to apply the theory to any specific situation.

One of the exceptions can be seen in the work of Ragozin and Brown (1985). Their paper *Harvest Policies and Non-market Valuation in a Predator-Prey System,* using the Pacific Halibut *(Hippoglos-sus stenolepis)* and a fictitious prey as an example, seeks to analyse the case where a prey with no commercial value can nonetheless be given an economic value if its predator has a harvest value. Noting the apparent dearth of research into optimal harvesting of interdependent fishery populations, Strobele and Wacker (1995) discuss the properties of a two species predator-prey model in the presence and absence of harvesting. The authors conclude that if a predator-prey system is harvested, the 'golden rule' of harvesting in the steady-state is changed by additional 'productivity effects'; moreover in the case where the predator is of value, the optimal stock of prey is always greater than in the corresponding single species model. Another to examine multiple species fisheries is Pradhan and Chaudhuri (1999), who model the problem of non-selective harvesting of a two species fishery where species are competing. These authors focus their attention on the use of taxation as an optimal instrument to control exploitation of the fishery.

The emergence of game ranches in southern Africa has led to the development of a small body of literature devoted to modelling the consumptive use of game. Van Kooten et al. (1997) use a dynamic stochastic simulation model of forage, herbivores, predators and domestic livestock in the Machakos District of Kenya to address policies relating to the multiple use of rangeland resources. In particular they seek to analyse the impact of the Kenyan Government permitting game ranchers to harvest wildlife and sell the meat for profit. Their results preclude them from drawing firm conclusions about the desirability of the new policy, concluding: "Depending on the ranchers' behaviour and attitudes to risk, introducing economic incentives may stabilise wildlife populations...", although "imposing economic incentives...on a traditional commercial ranching system may not always lead to an ecologically and economically preferred outcome" (van Kooten et al., 1997, p.461).

Extending the analysis to examine a variety of potential wildlife conservation policies, (Kinyua et al., 2000) conclude that allowing uncontrolled harvesting and sale of wildlife, coupled with the requirement that ranchers maintain wildlife populations at or above a pre-set level, presents the best policy from the standpoint of wildlife conservation and ranch returns. Hearne et al. (2000), leaving conservation issues aside, presents a detailed sex-and age-structured model designed to optimise the consumptive use of game from the perspective of a private game rancher.

As game ranches contain a number of species, the models discussed above invariably take a multiple species approach. However, the bioeconomic literature does not contain a generalised multiple species model for the conservation of terrestrial species. This thesis seeks to redress this omission.

2.2 A Closer Look at the Models of Extinction

2.2.1 The Clark Single Species Model

In a situation in which the owner is seeking to maximise static rent (net revenue) from the resource, Clark determines that in all cases, irrespective of the relative price to the cost of harvest, an optimal positive stock level results, that is, static rent maximisation never leads to extinction. However, when the problem becomes one of maximising the present value of net revenue streams, Clark demonstrates that if the price exceeds the cost of harvest for all stock levels, and the discount rate is sufficiently large, then the potential for extinction exists.

Clark (1973) posits a societal objective function of maximising the present value of the net returns from the resource as follows:[9]

$$\underset{h}{Max} \int_0^{\infty} e^{-\delta t} \left[p(h(t))h(t) - c(x(t))h(t) \right] dt \tag{2.1}$$

$$s.t. \quad \dot{x} = F(x(t)) - h(t),$$

where $x(t)$ is the stock level of the species in time t, $\dot{x}$ is the derivative of x with respect to time, $h(t)$ is the harvest of the species in time t, $p(h(t))$ is the inverse demand curve defined as a function of harvest, $c(x(t))$ is the unit of cost of harvest as a function of stock, and δ is the societal discount rate. For convenience of exposition, the time notation will subsequently be suppressed, but will be understood to be implicit in all control and state variables for the remainder of this thesis.

---

[9] For notational consistency with the models below, we use Clark's (1976) interpretation of Clark (1973).

Consistent with economic theory, in order to maximise its investment across all assets, a society will seek to hold each asset at a level that equates their marginal returns.[10] The condition associated with optimal harvest (h^*) is shown in Equation (2.2), and that associated with optimal stock levels (x^*) is shown in Equation (2.3).

$$\lambda = p\left[\frac{1}{\varepsilon_d}+1\right]-c \tag{2.2}$$

$$\delta = F'(x)-\frac{c'(x)h}{p(h)-c(x)}, \tag{2.3}$$

where λ is the shadow value of the resource, and ε_d is the elasticity of demand for the resource. Equation (2.3) represents a modified version of the *golden rule* equation common in natural resource applications. The original golden rule, $\delta = F'(x)$, suggests the resource should be maintained at a stock level such that the returns to capital available to the resource owner, δ, are equal to the marginal productivity of the renewable resource stock, $F'(x)$.

In this modified form, Equation (2.3) implies that the returns to the resource are dependent upon two factors: the growth rate and the cost of harvest (which is a decreasing function of stock, $c(x)<0$). This modification therefore increases the effective marginal productivity of the stock relative to the discount rate, making the stock a more attractive investment.

The policy implications are straightforward. Extinction results from low growth rates and high price-cost (of harvest) ratios. Given that the policymaker's ability to alter the growth rate of a natural resource is limited, the policy response must focus on the price-cost ratio. As Swanson (1994) points out, this is the mechanism by which policies such as a CITES trade ban works. By effectively removing the value of harvest, policymakers create a more favourable price–cost ratio for the species in question.

---

[10] The argument is as follows: if there exists two assets, one with a higher marginal return than the other, gains can be made from increasing your holdings of the asset earning the higher return at the expense of the alternative asset. These gains will exist until such point where the marginal returns across the assets are equal.

2.2.2 The Clark Multiple Species Model

Clark (1990), acknowledging that it is rare for a fishing vessel to exploit a single species of fish, seeks to develop a bioeconomic model of a mixed-species fishery. Clark defines a multiple species fishery as one in which more than one species is caught simultaneously by a single fishing technique (Clark cites the example of bottom trawling, where various species are captured in the trawl nets).

Making the assumption that the two species x_1 and x_2 are ecologically independent, Clark gives population growth functions for each species as follows:

$$\dot{x}_1 = F(x_1) - q_1 E x_1$$

$$\dot{x}_2 = G(x_2) - q_2 E x_2$$

where, x_1 and x_2 are the populations of species 1 and 2 respectively, E (fishing effort) is assumed to be equal across species, but the corresponding fish mortalities $q_2 E x_1$ and $q_2 E x_2$ may differ due to different catchability coefficients q_1 and q_2.

The possible equilibria of the above model $(\dot{x}_1 = \dot{x}_2 = 0)$ are given by

$$\frac{F(x_1)}{q_1 x_1} = \frac{G(x_2)}{q_2 x_2} = E$$

Under an open-access regime, if species 1 has a larger (biological) growth rate to catchability ratio than that of species 2, the elimination of the second species becomes possible; that is, providing species 1 is sufficiently valuable, the fishery may remain viable, even though the valuable, but less productive species 2 is ultimately fished out.

In the case where the resource has a single owner, and excluding the possibility of selective fishing, the resource manager has two options 1) limit the total catch, so as to protect the vulnerable species, or 2) allowing fishing of other species to proceed, effectively 'writing off' the vulnerable species.

Clark posits an objective function (with zero discounting) as follows:

$$\underset{E}{Max} \int_0^\infty \left[(p_1 q_1 x_1 + p_2 q_2 x_2 - c) E \right] dt \qquad (2.4)$$

$$s.t. \quad \dot{x}_1 = F(x_1) - q_1 E x_1 = 0$$

$$\dot{x}_2 = G(x_2) - q_2 E x_2 = 0,$$

where, p_1 and p_2 are the price of harvest for species 1 and 2 respectively, c is the cost of harvest, and all else is as previously defined.

In this situation, and continuing to assume species 2 has the lower growth rate, the end result depends upon the relative prices of the two. If species 2 is highly priced $(p_2 > p_1)$, the optimum effort is largely determined by species 2, and species 1 is harvested primarily as a by-catch. This results in positive equilibrium population levels of both species. If, however, species 1 is the highly priced species, the optimum effort is entirely determined by the parameters of the first species. Here species 2 constitutes the by-catch, but may be progressively eliminated, resulting in the extinction of the second species.

2.2.3 The Swanson Model

Swanson (1994) develops a generalised model of extinction based upon the observation that humans do not compete for many of the ocean resources used by marine species, yet they do compete for the same land-based resources used by terrestrial species.

Swanson considers species extinction to be the result of the species not being included in the human asset portfolio; that is, human societies select a portfolio of assets from which to derive a flow of benefits. Natural assets are simply a subset of all the potential assets from which humans must choose. Therefore, the problem of specific species extinction and biodiversity loss in general stems from society's choice to convert these natural assets into those generating a higher return. These alternatives may take the form of man-made capital assets, or other quasi-natural assets, such farmland.

Although exclusion from the human asset portfolio is the fundamental force driving species to extinction, it is not the force that acts directly upon the species to bring about its decline. Swanson identifies three distinct such direct 'consequential' forces. First, 'stock-disinvestment' or 'resource mining' is where the species may be seen as immediately valuable, but not as a resource with potential for growth. Therefore, it will be perceived to be optimal to harvest the entire species stock in order to invest the return in another, more productive asset. This is the scenario developed by Clark (1973).

Second, a species may not be perceived to have sufficient value to be worthy of substantial investments in the supplementary resources required for its survival, the most obvious resource being land. When a species is not included in society's asset portfolio, then the allocation of base resources upon which it is dependent for survival are often diverted to another use. This is termed 'base resource allocation'. Third, the species may be seen as valuable, but not valuable enough to justify the allocation of resources required for its management. Again the species will experience disinvestment, but in this case the disinvestment occurs because of a lack of management of access to the species or its habitat. This is termed 'management service re-allocation'. Each of the three consequential forces has the same observable effect: species decline.

To take into account the need for terrestrial species to be allocated base (land) resources and working from both the Clark (1973) model above and the Solow model of asset substitution (1974), Swanson adds another control variable to the societal objective function Equation (2.1), which represents the land resources allocated to a species as shown in Equation (2.5) below:

$$\underset{h}{Max} \int_0^\infty \left[p(h)h - c(x)h - \delta \rho_L L \right] dt \tag{2.5}$$

$$s.t. \quad \dot{x} = F(x;L) - h,$$

where L is a unit of terrestrial resources upon which the species depends for survival, and ρ_L is the price of a base unit of that land resource. This formulation removes the implicit assumption in fisheries-based models that the resources required for a species survival are free goods that do not require investment. This generates one of Swanson's 'alternative routes to extinction' through the addition of another first order condition:

$$\delta = \frac{\lambda H_L}{\rho_L}, \tag{2.6}$$

where H_L is the change in population growth associated with a change in resources provided to the population. Similar in concept to the golden rule equilibrium discussed above, this condition requires that land-based resources be allocated to a species only in proportion to its ability to generate a competitive return to those resources. Note that this condition is in addition to the ones shown in Equations (2.2) and (2.3) above. The species in question must not only be capable of generating a competitive return on its own stock value, but must also be able to earn a competitive return on the additional resources that it needs to survive.

This result has significant implications for policy. While the Clark model advocates protecting species from extinction through reducing the price-cost of harvest ratio. Swanson's model suggests the opposite. For terrestrial species at least, the species must be able to generate a sufficient return to afford a competitive rate of return on the resources it needs for survival. Therefore, policies such as the CITES ban, while reducing the threat of a species being harvested to extinction, increase the likelihood of undermining the specie's ability to generate a competitive return on its base resources. The species simply moves onto 'an alternative (albeit slower) path to extinction'.

CHAPTER III

INTRODUCING MULTIPLE SPECIES INTO THE BIOECONOMIC FRAMEWORK

3.1 The Growth Function

The models given in the previous chapter present an unspecified growth function of the renewable resource stock, $F(x)$. Any account of population dynamics should begin with a description of the kind of population growth known as geometric, exponential, or Malthusian (after the writings of Thomas Malthus discussed earlier). In an unlimited environment, population growth will follow a simple geometric progression as the full natural rate of increase of that population. The growth of such a population, x, can be very simply described by a differential equation $\dot{x} = rx_t$, where the rate of change of the population over time equals the product of the natural (intrinsic) rate of increase, r, and population size at any instant, x_t. The term r is important in population biology, referring to the instantaneous per capita rate of population growth. The value of r depends on the individual birth and death rates in the population. $r = b_0 - d_0$ where b_0 and d_0 represent the average number of births and deaths per individual per unit time, respectively. The subscripts refer to the fact that these rates are measured when the population is very small.

Such growth clearly cannot be maintained indefinitely; as resources become limiting, intraspecific competition has a dampening or depressive effect on such free growth. Incorporating a second term to represent this dampening effect, we have the logistic growth function developed by Verhulst (1838) and later and independently by Pearl (1925) (Pielou, 1974; Clark, 1976; Putman, 1994):

$$F(x) = \dot{x} = rx\left[1 - \frac{x}{K}\right], \tag{3.1}$$

where K is the carrying capacity of the habitat. This function yields a sigmoidal growth curve of the population in question. It is straightforward to interpret biologically what the model is doing mathematically by considering what will happen to our population as the ratio of x to K changes. Where $x < K$ and thus population size is below its carrying capacity, $\frac{x}{K}$ is less than one, the function

$\left(1-\frac{x}{K}\right)$ is thus greater than zero and the population will increase in size. Indeed, when x is very small, $\frac{x}{K}$ tends to zero and the population will realise its full intrinsic rate of increase, with no dampening effect of intraspecific competition experienced. Where $x = K$ the population will remain stable $\left(1-\frac{x}{K}\right) = 0$ (thus the rate of growth is zero). Where $x > K$, the population will decline (Putman, 1994).

The application of the logistic growth equation requires three assumptions: 1) That all individuals are equivalent 2) That K and r are fixed constants independent of time, sex, and age distribution and 3) That there is no time lag in the response of the actual rate of increase per individual to changes in x. All three assumptions are unrealistic and can be strongly criticised (Jorgensen et al., 1996).

Nevertheless, a number of population phenomena can be nicely illustrated, and most of the growth functions present in the literature are built upon this base. For our purposes the enhanced ecological realism obtained from the specification of a more complex growth function is offset by the resulting reduction in expositional clarity. For this reason, the function specified in Equation (3.1) serves to illustrate population growth in our single species model.

Ecological communities however are composed of many populations of distinct species interacting to varying degrees. The potential interactions range from essentially neutral interactions in which two populations are jointly part of each other's habitat but not part of each other's environment, to interactions with some direct influence on the ability of the individuals in one or both populations to survive and reproduce. Clearly these interactions need to be considered when attempting to build models within a multiple species framework.

3.2 Dealing with Multiple Species

Into the logistic growth function given by Equation (3.1) above, it is possible to incorporate a further function to represent the effects of interspecific interaction. Following Putman (1994), in its simplest form this term is calculated to include an effect from the size of the population of the interacting species x_2, and an interaction coefficient α, representing the strength of interaction by altering the extent to which the growth rate of species 1 is influenced by the presence of a given number of species 2.

Our equation for population growth of species 1 now becomes:

$$F(x_1, x_2) = \dot{x}_1 = r_1 x_1 \left[1 - \frac{x_1}{K_1}\right] + r_1 x_1 \left[\alpha_{1,2} \frac{x_2}{K_1}\right] \tag{3.2}$$

or:

$$F(x_1, x_2) = \dot{x}_1 = r_1 x_1 \left[1 - \frac{x_1}{K_1} + \alpha_{1,2} \frac{x_2}{K_1}\right] \tag{3.3}$$

where $\alpha_{1,2}$ represents the relative impact of one individual of species 2 on the population growth rate of species 1. K_1 appears in the denominator throughout since we are interested in the effects of both intraspecific and interspecific competition on resources used by species 1. If $\alpha_{1,2}$ is greater than one, an individual of species 2 has more influence on the growth rate of species 1 than does a single individual of species 1.

The growth of species 2 can equally be described as:

$$G(x_1, x_2) = \dot{x}_2 = r_2 x_2 \left[1 - \frac{x_2}{K_2} + \alpha_{2,1} \frac{x_1}{K_2}\right] \tag{3.4}$$

Clearly these simple equations can be extended to accommodate interaction with more than one interacting species. Additional elements may be added to represent the additional effects of a third, fourth or fifth species.

Simply altering the sign of the interaction component $\left(\alpha_{i,j} \frac{x_j}{K}\right)$ of the population growth function allows us to represent all the various relationships, through which various members of a community might interact. A mutually beneficial relationship results in both components having a positive effect, a predator-prey relationship has one positive (predator's growth) and one negative (prey's growth), and interspecific competition has both components negatively affecting growth.[11]

---

[11] This approach follows convention, in that rather than specifying positive or negative interaction coefficients, all coefficients are deemed positive, with their effect on growth determined by the specification of the growth function.

The analyses developed here upon a logistic model of population growth were first suggested by Lotka (1925) and Volterra (1926). It is their work upon which these simple equations are based. It should be emphasised that the Lotka-Volterra equations greatly oversimplify the processes of population growth and interaction; for example, the model considers all members of the population to be equivalent. No account is taken of age structure or possible age-specific differences in fecundity or survival. In addition, the model (as presented) is restricted to analysing the dynamics of populations exhibiting continuous growth. For models of populations with discontinuous growth, see Leslie (1945; 1948) or Hassell (1975), and for age-structured populations, Gurney, et al. (1983). Nevertheless, the basic logic of these models is essentially the same (Putman, 1994).

3.3 The Ecology of Species Interaction

The field of community ecology is dominated by the study of species interaction. The two fundamental interactions among species are considered to be competition and predation, although the relative importance of each is an area of controversy. Other potential interactions include Mutualism (beneficial to both species), Commensalism (beneficial for one species, neutral for the other), Amensalism or Allelopathy (detrimental to one species, neutral for the other) and Parasitism (positive for one species, negative for the other) (McNaughton and Wolf, 1979; Stiling, 1992).

A key question in the study of species interaction is how to define 'interaction'. Two definitions exist: the first is defined on the individual level, in terms of the relative health of organisms that do and do not participate in the interaction. The second definition considers the effect at population level and is measured by the change in the growth rate of population 1 as population 2 changes. While the former definition is appropriate for questions of evolution, it is inadequate when considering population-level phenomena. For example, many frugivorous animals destroy some of the seeds they consume and disperse others; the net result of these individual predations and mutualisms may be either an increase or a decrease in the plant population (Boucher et al., 1982).

The population level definition is tacitly assumed in the Lotka-Volterra type analysis, and consequently is the definition employed here. I consider three cases of species interdependence: 1) independent species, 2) species competition, and 3) a predator-prey relationship. Interspecific competition and predator-prey relationships are considered as they are the interspecific relationships, which dominate most ecosystems. Independent species are considered because of the interesting economic implications that arise.

3.3.1 Independent Species

The case of two species coexisting, yet not interacting, within a single habitat is unsurprisingly given little attention in ecological modelling. Indeed, if species 1 and 2 are ecologically independent, there exists little ecological motivation to model them jointly. In this case two single species models, one for species 1 and one for species 2, would seem to be not only intuitive, but sufficient. Thus, our multiple species population growth model would simply revert to a single species model as given by Equation (3.1).

However, being ecologically independent does not necessarily imply the species are economically so. For this reason, the case of two independent species is introduced, albeit briefly at this stage.

3.3.2 Competition

Few subjects elicit as much controversy in community ecology as interspecific competition. Until the mid-to-late 1970s the view that competition was the dominant force shaping ecological communities was prevalent, at which time many authors began to voice dissent. Among those who reject interspecific competitions dominance, two extreme positions can be distinguished. One advocates strong biological interaction, but asserts that predation is far and away the most prevalent of these. A second position de-emphasises strong biological interactions of any kind (see, for example, Connell et al., 1970). In response, Connell (1983) and Schoener (1983) independently sought to review the literature for evidence of the existence of interspecific competition.

The former, taking a sample of published studies that used field experiments designed to detect the existence of competition, concluded that in a sample of competition studies covering 215 species, competition was found in more than half of the species. Of the experiments that distinguished intraspecific from interspecific competition, interspecific competition was found to be the stronger in about one-sixth (Connell, 1983). Schoener (1983) collates results from all field experiments on interspecific competition in the literature. Competition was found in 90 percent of the studies and 76 percent of the species. The experiments conclude unequivocally that interspecific competition has been established in a great variety of natural systems and among a great variety of organisms. Furthermore, no significant difference was found between ecological systems: 91 percent of freshwater, 94 percent of marine, and 89 percent of terrestrial studies show some competition. On this evidence, Schoener is able to reject the argument against the prevalence of interspecific competition.

Dissenters notwithstanding, there is general agreement that while competition is undoubtedly a dominant ecological force, its dominance is not as complete as originally supposed (McNaughton and Wolf, 1979; Stiling 1992; Krohne, 2001). As with many ecological terms, no unique definition of competition exists. Here competition is said to exist where there is a negative biological interaction occurring between two or more individuals when (1) a necessary resource is in limited supply relative to species demands or (2) resource quality varies and demand is greater for higher quality resources. This definition expands the common concept that competition is for a resource in short supply to include attempts to utilise different qualities within a resource type (Stiling, 1992).

Competition is an active process that has major influences on the ability of competing individuals to survive and reproduce. The types of influence can vary from 1) direct interference with access to a resource (interference competition) to 2) reducing the availability of a resource and thus the efficiency of exploitation of that resource (exploitation competition) (McNaughton and Wolf, 1979). Although in ecological modelling interference and exploitation competition are often treated separately, the two will be combined.

The prevalence of competitive interactions in nature indicates that the net result of interspecific competition is rarely extinction of the less competitive species. In the simplest coexistence model, both species have non-zero populations that are no longer changing. Thus we are interested in positive populations of the two species such that $\dot{x}_1$ and $\dot{x}_2 = 0$. Specifying the competitive forms of Equations (3.3) and

(3.4), and following the analysis of Lotka (1925) and Volterra (1926), we are able to determine the conditions under which competitive coexistence is possible.

Setting $\dot{x}_1$ and $\dot{x}_2 = 0$ yields the following zero isoclines:

$$K_1 - x_1 - \alpha_{1,2}x_2 = 0 \tag{3.5}$$

$$K_2 - x_2 - \alpha_{2,1}x_1 = 0 \tag{3.6}$$

From (3.5) we can see that the population of species 1 will decline when $x_1 > K_1 - \alpha_{1,2}x_2$, remain constant when $x_1 = K_1 - \alpha_{1,2}x_2$, and increase when $x_1 < K_1 - \alpha_{1,2}x_2$. A similar deduction can be made from (3.6) for species 2.

Plotting (3.5) and (3.6) in x_1, x_2 space, we have four possible outcomes: 1) Extinction of species 1; 2) Extinction of species 2; 3) Extinction of either species 1 or 2 (unstable equilibrium); or 4) Coexistence.

Restricting our attention to the fourth case (for further analysis of the other cases see McNaughton and Wolf, 1979; Stiling 1992; and Krohne, 2001). This leads us to the question; under what conditions is coexistence possible? In order for the isoclines to appear as in Figure 3.1 (p.45), $K_1 < \left(\dfrac{K_2}{\alpha_{2,1}}\right)$ and $K_2 < \left(\dfrac{K_1}{\alpha_{1,2}}\right)$. Rearranging, we see that $\alpha_{2,1} < \left(\dfrac{K_2}{K_1}\right)$ and $\alpha_{1,2} < \left(\dfrac{K_1}{K_2}\right)$. For this to be the case, the competitive coefficients (alphas) must be small. In particular, for both species the effect of the competitor must be small relative to the ratio of the carrying capacity to that of the other species. Those conditions must hold for both species simultaneously, and this is possible only if the carrying capacities of the two species are similar such that their ratio, regardless of which is the numerator is close to one, thus any great disparity in the carrying capacities of the two species will result in competitive exclusion, or a non-stable equilibrium. In summary, stable coexistence in this graphical analysis occurs under conditions that make intuitive sense: small values for alpha and large carrying capacities for both species (Krohne, 2001).

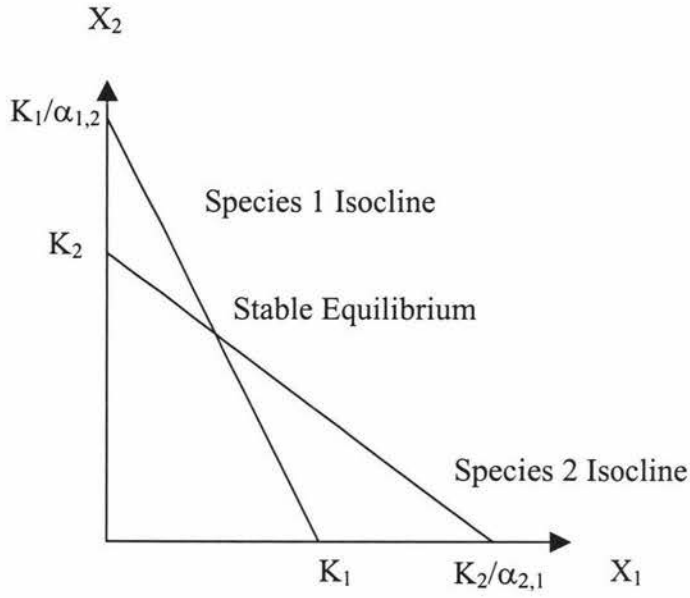

Figure 3.1: Stable Equilibrium between Two Competing Species

(Source: Krohne, 2001).

3.3.3 Predator-Prey

Ecologists have long recognised the potential importance of predation in influencing population growth. A predator in the broadest sense of the word is any organism that eats all or parts of other live organisms, the prey. By this definition, any organism that eats another is a predator, including herbivores as well as carnivores (McNaughton and Wolf, 1979). For modelling purposes, however, the definition is restricted to an animal whose feeding removes individual prey from a population; on the basis that an individual prey removed no longer depletes the resources available to the prey population nor contributes to its growth.

Much of the ecological literature is devoted to studying the individual level evolutionary effects predation has on both the predator and prey species. A predator must find, recognise, capture and consume its prey. To this end predators are often distinguished by their acute sensory perception, whether sight, smell or sound. Prey, however, develop adaptations to counter those of their predators. These adaptations consist of avoiding one or more of the three categories of the predator's efforts: detection, capture or handling (Krohne, 2001).

Of more interest to us are the population level effects. Predation is known to play an important role in organising ecological communities. Its contribution is less controversial than that of competition, both because few ecologists claim that predation is as dominant an organising force as competition, and because many field experiments have demonstrated its importance (Schaller, 1972; Sinclair, 1985; Mills and Shenk, 1992).

First consider the effect of changing predator populations upon prey species. Paine's (1966) classic work, studying the effect removal of the carnivorous Starfish (*Pisaster ochraceous*) has upon its invertebrate prey, gave rise to the Keystone Predator hypothesis, where a single predator is the central species to the organisation of an entire community. This hypothesis has implications for the question over the relationship between diversity and ecosystem stability. The existence of keystone species indicates that it may not always be possible to make predictions about stability and diversity. Clearly the elimination of keystone species may have greater consequences than the loss of some other species (Krohne, 2001)

Turning to the effect of changing prey populations upon predator species, consider the potential responses of a predator to an increase in the density of its prey. Each predator can either consume more prey (the functional response) or the number of predators can increase (the numerical response). Holling (1959) demonstrates an inverse relationship between the two for any one species. A large numerical response is associated with a small functional response and vice versa. Hence, understanding the functional response is crucial when using predators to control prey populations.

As with interspecific competition, the prevalence of predator-prey interactions in nature indicates that the net result is rarely extinction of prey by virtue of the action of the predator; some form of coexistence seems to be the norm (Krohne, 2001). Returning to Equations (3.3) and (3.4), and again following the analysis of Lotka (1925) and Volterra (1926), we are able to determine the conditions under which coexistence is possible.

Letting x_2 represent the predator population, and setting $\dot{x}_1 = 0$ we have:

$$\dot{x}_1 = r_1 x_1 \left[1 - \frac{x_1}{K_1} + \alpha_{1,2} \frac{x_2}{K_1} \right] = 0,$$

which yields,

$$K_1 - x_1 + \alpha_{1,2}x_2 = 0, \tag{3.7}$$

similarly for x_2 (prey) we have:

$$\dot{x}_2 = r_2 x_2 \left[1 - \frac{x_2}{K_2} - \alpha_{2,1}\frac{x_1}{K_2}\right] = 0,$$

which yields,

$$K_2 - x_2 - \alpha_{2,1}x_1 = 0 \tag{3.8}$$

Equations (3.7) and (3.8) represent two linear isoclines $\dot{x}_1 = 0$ and $\dot{x}_2 = 0$. Restricting our attention to cases where $K_1 < \left(\frac{K_2}{\alpha_{2,1}}\right)$ and $K_2 < \left(\frac{K_1}{\alpha_{1,2}}\right)$ yields a single equilibrium population of each species depicted at the intersection of the isoclines in Figure (3.2) (p.47). As aforementioned, this is the simplest of cases; for a more in-depth analysis of predator-prey population dynamics see Krohne (2001).

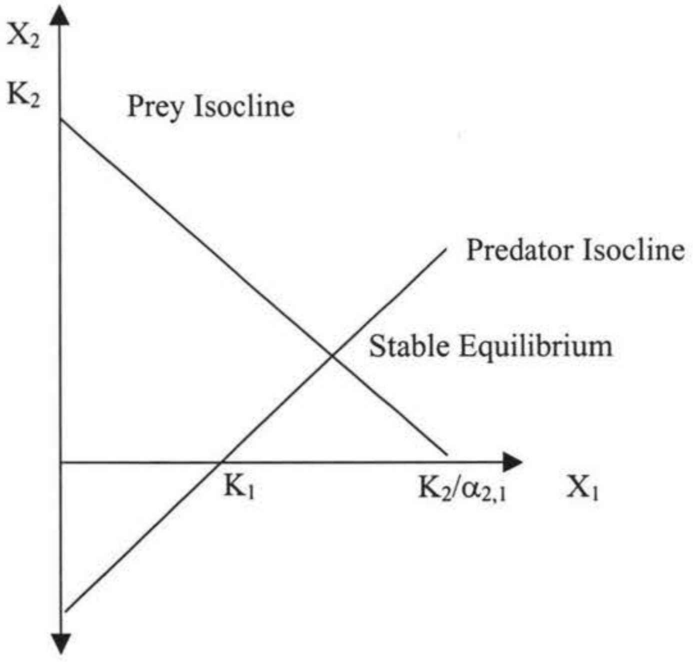

Figure 3.2: Stable Equilibrium between a Predator and Prey

(Source: Krohne, 2001).

3.4 The Economics of Species Interaction

Production economics is concerned with choice among alternative production processes. How much and what to produce and the optimal combinations of resources are key issues in any production problem, whether at the level of an individual firm, an entire industry, or society. Explicitly, *production* can be defined as:

> ...the process of combining and coordinating materials and forces (inputs, factors, resources, or productive services) in the creation of some good or service (output or product).
>
> (Beattie and Taylor, 1985, p.3)

An abstract representation of the production process is given by the *production function*, defined as:

> ...a quantitative or mathematical description of the various technical production possibilities faced by a firm. The production function gives the maximum output(s) in physical terms for each level of the inputs in physical terms.
>
> (Beattie and Taylor, 1985, p.3)

In this context, land resources and existing species can be viewed as inputs, and additional species as outputs. The growth functions specified above are analogous to production functions in general economic theory.

Production economics literature makes clear the distinction between firms producing single outputs and those producing multiple outputs (Beattie and Taylor, 1985). To the extent that the allocation of land resources for conservation of one species necessarily provides habitat to other species that share that land, conservation management may be viewed as a multiple product production process. Multiple product production can generally be viewed as production of several single products, but with the products linked through resource constraints, non-allocable factors of production and/or through jointness in production. To recognise this relationship within the bioeconomic framework, it is necessary to specify multiple product production functions.

Within multiple product production, distinction is drawn between joint and non-joint production; joint production is said to exist when more than one output emerges from a single productive activity. Adam Smith (1776) illustrates this notion by the example of hunting, where meat and skins of some animals are produced together at the same time and in fixed proportion. A more modern example is the refinement of crude oil, which yields a number of different products, such as petroleum, motor oil and kerosene. Two classes of joint production are distinguished in the literature: the case where all joint products are desirable, and the case where one product is desirable while another is undesirable (Baumgartner et al., 2001). The latter case is well documented in the ecological economic literature, early authors including Johann Heinrich von Thumen, William Jevons and Karl Marx; all address the phenomenon of pollutants arising as joint products of desired goods (Baumgartner, 2000).

While well studied in production economics, the case where all joint products are desirable has received little attention in natural resource economics. However, Baumgartner et al. (2001) have recently suggested joint production, although not recognised as such, is in fact a fundamental concept in ecology. They argue that ecosystems "...as open, self-organising systems, necessarily take in several inputs and generate several outputs..." (p.367). Although it is by no means the case that all species are at all times desirable, it is a working assumption in this thesis that the conservation problem is one in which that assumption may hold. Thus, the case of undesirable species, such as exotic species, will not be explicitly addressed in this work.

A further distinction found in the literature is between allocable and non-allocable factors of production. Non-allocable factors are those for which the amount of the factor of production Z used in producing a given output Y_1 cannot be distinguished from the amount of that factor used in producing output Y_2. Using this notation, Y_1 and Y_2 would both be produced by the same units of factor Z. Another way of looking at a non-allocable factor is that as Z is employed in producing Y_1, then one also gets some Y_2 output, whether desired or not. An often-cited example is that of mutton and wool being produced from feeding sheep (Beattie and Taylor, 1985).

Where the factor under consideration is conservation land, clearly we have a case of a non-allocable factor. Once a conservation area has been established, the area is freely available for use by each species living within it. The case of joint production with non-allocable factors of production is illustrated in Figure 3.3 (p.50).

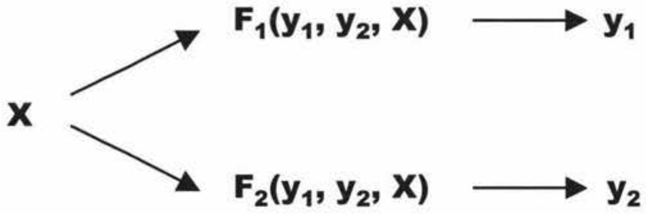

Figure 3.3: A Non-allocable Factor of Production

(Source: Adapted from Beattie and Taylor, 1985)

where X represents the total quantity of input (land), and $F_1(.)$ and $F_2(.)$ represent the production functions through which X is converted into outputs y_1 and y_2 (species 1 and 2) respectively.

3.5 The Multiple Species Model

In this chapter, a simple two species model is developed to demonstrate the effect of adding additional species to the single species bioeconomic framework.

3.5.1 The Analytical Model

Beginning analytically, suppose society wishes to maximise the present value of net returns from harvesting both species. Noting that time notation has been suppressed but is understood to be implicit in all control and state variables, the objective function may be specified as:

$$\max_{h} \int_0^\infty e^{-\delta t}\left\{\left[p_1 - c_1(x_1)\right]h_1 + \left[p_2 - c_2(x_2)\right]h_2 - \delta p_L L\right\} \tag{3.9}$$

where subscripts denote species 1 and 2, L is a unit of terrestrial resource (land) upon which the species depends for survival, and p_L is the unit price of a base unit of that land resource. Following Swanson (1994), this term is multiplied by the social discount rate, δ, to indicate that the returns from our two species must match the opportunity cost of alternative returns available from use of the same land. For transparency, the inverse demand function of the standard bioeconomic model, $p(h)$, has been replaced by fixed prices p_1 and p_2. All other notation is as previously indicated.

The dynamics defining the stock of each species are represented by the state equations:

$$\dot{x}_1 = F\left(x_1, x_2, L\right) - h_1 \tag{3.10}$$

$$\dot{x}_2 = G\left(x_1, x_2, L\right) - h_2 \tag{3.11}$$

where $F\left(x_1, x_2, L\right)$ and $G\left(x_1, x_2, L\right)$ are the joint production functions of species 1 and 2, where the land resource, L, is non-allocable.

The current value Hamiltonian is:

$$\begin{aligned} H = {} & [p_1 - c_1(x_1) - \lambda_1]h_1 + [p_2 - c_2(x_2) - \lambda_2]h_2 - \delta p_L L + \lambda_1 F(x_1, x_2, L) \\ & + \lambda_2 G(x_1, x_2, L) \end{aligned} \tag{3.12}$$

The Pontryagin necessary conditions for a maximum are:

Optimality equations

$$\frac{\partial H}{\partial h_1} = p_1 - c_1(x_1) - \lambda_1 = 0 \tag{3.13}$$

$$\frac{\partial H}{\partial h_2} = p_2 - c_2(x_2) - \lambda_2 = 0 \tag{3.14}$$

$$\frac{\partial H}{\partial L} = -\delta p_L + \lambda_1 F_L + \lambda_2 G_L = 0 \tag{3.15}$$

Co-state equations

$$\frac{-\partial H}{\partial x_1} = -[-c_1'(x_1)h_1 + \lambda_1 F_1 + \lambda_2 G_1] = \dot{\lambda}_1 - \delta\lambda_1 \tag{3.16}$$

$$\frac{-\partial H}{\partial x_2} = -[-c_2'(x_2)h_2 + \lambda_1 F_2 + \lambda_2 G_2] = \dot{\lambda}_2 - \delta\lambda_2 \tag{3.17}$$

State equations

$$F(x_1(t), x_2(t), L(t)) - h_1(t) = 0 \tag{3.18}$$

$$G(x_1(t), x_2(t), L(t)) - h_2(t) = 0 \tag{3.19}$$

and the usual transversality and boundary conditions.

Solve Equations (3.13) and (3.14) for λ_1 and λ_2 respectively

$$\lambda_1 = p_1 - c_1(x_1) \tag{3.20}$$

$$\lambda_2 = p_2 - c_2(x_2) \tag{3.21}$$

Now take d/dt of Equations (3.20) and (3.21)

$$\dot{\lambda}_1 = -c_1'(x_1)\dot{x}_1 \tag{3.22}$$

$$\dot{\lambda}_2 = -c_2'(x_2)\dot{x}_2 \tag{3.23}$$

Substitute Equations (3.20) and (3.21) into (3.22)

$$-\delta p_L + [p_1 - c_1(x_1)]F_L + [p_2 - c_2(x_2)]G_L = 0 \tag{3.24}$$

Substitute Equations (3.20), (3.21), (3.22) and (3.23) into Equations (3.16) and (3.17)

$$c_1'(x_1)h_1 - [p_1 - c_1(x_1)]F_1 - [p_2 - c_2(x_2)]G_1 = c_1'(x_1)\dot{x}_1 - \delta[p_1 - c_1(x_1)] \tag{3.25}$$

$$c_2'(x_2)h_2 - [p_1 - c_1(x_1)]F_2 - [p_2 - c_2(x_2)]G_2 = c_2'(x_2)\dot{x}_2 - \delta[p_2 - c_2(x_2)] \tag{3.26}$$

Assume a system in equilibrium such that all conditions are met simultaneously. Let $\dot{x} = 0$ at equilibrium, by definition, so that $-c_1{}'(x_1)\dot{x}_1 = 0$ and $-c_2{}'(\mathrm{x}_2)\dot{x}_2 = 0$. Further, let $h_1 = F(x_1, x_2, L)$ and $h_2 = G(x_1, x_2, L)$ at equilibrium from Equations (3.18) and (3.19). Given these assumptions, solve Equations (3.24), (3.25) and (3.26) for δ.

$$\delta = \frac{[p_1 - c_1(x_1)]F_L}{p_L} + \frac{[p_2 - c_2(x_2)]G_L}{p_L} \tag{3.27}$$

$$\delta = F_1 - \frac{c_1'(x_1)F(x_1, x_2, L)}{[p_1 - c_1(x_1)]} + \frac{[p_2 - c_2(x_2)]}{[p_1 - c_1(x_1)]}G_1(x_1, x_2, L) \tag{3.28}$$

$$\delta = G_2 - \frac{c_2'(x_2)G(x_1, x_2, L)}{[p_2 - c_2(x_2)]} + \frac{[p_1 - c_1(x_1)]}{[p_2 - c_2(x_2)]}F_2(x_1, x_2, L) \tag{3.29}$$

Let unit net revenue from species i be denoted $R_i = \left[p_i - c_i(x_i)\right]$ and substitute into (3.27), (3.28) and (3.29).

$$\delta = \frac{R_1 F_L}{p_L} + \frac{R_2 G_L}{p_L} \tag{3.30}$$

$$\delta = F_1\left(x_1, x_2, L\right) - \frac{c_1'\left(x_1\right)F\left(x_1, x_2, L\right)}{R_1} + \frac{R_2}{R_1}G_1\left(x_1, x_2, L\right) \tag{3.31}$$

$$\delta = G_2(x_1, x_2, L) - \frac{c_2'(x_2)G(x_1, x_2, L)}{R_2} + \frac{R_1}{R_2}F_2(x_1, x_2, L) \tag{3.32}$$

It is assumed throughout that $R_1, R_2 > 0$ for all relevant levels of x_1, x_2, otherwise the cost of harvest would exceed the revenues and no harvest would occur. Equation (3.30) reflects the impact of the land control term in the objective function, and is a multiple species version of the result found by Swanson (1994). This condition implies that society will allocate land only to the extent that the species supported by it are able to generate a competitive rate of return from their use of the resource. In a single species model, it would appear that this return must be generated entirely by the species under consideration. However, when the conservation of a wilderness area provides benefits to many species, the returns generated by all species may contribute to meeting the required returns from the land resource.

Although attention is restricted to the two species case, the extension to multiple species will simply lead to additional terms on the right hand side (RHS), resulting in a further reduction of individual species burden. This relationship holds regardless of the nature of any interdependence between the species.

Equations (3.31) and (3.32) are modified golden rule equations for species 1 and 2 respectively, analogous to that shown in Equation (2.3). Recall that the left hand side (LHS) and the first term on the RHS indicate that the resource must be maintained at a stock level such that the marginal productivities of the resource stocks, F_1 and G_2, equate to the return available from other assets δ. All other terms on the RHS modify that relationship.

The second terms on the RHS of Equations (3.31) and (3.32) reflect the stock-dependent harvest costs ($c'(x) < 0$), expressed proportionately to the unit net revenue of harvesting the resource. The only adjustment from the single species case is that the growth functions, $F(x_1, x_2, L)$ and $G(x_1, x_2, L)$, are now potentially interdependent. As before, this term acts to increase the marginal productivity of the resource, making the resource a more attractive investment. While these terms exhibit potential interdependence between species, they arise directly from the harvest activity and are strongly dependent on the ratio of marginal costs to marginal revenues.

The third terms on the RHS of Equations (3.31) and (3.32) reflect the biological interdependence of the two species, modified by the relative marginal profitability of each. Each equation indicates that returns for one species are modified by the marginal affect that species has on the other, times the proportional revenue of the other species to the first. Whether this makes a species more or less desirable in the human asset portfolio depends upon both the ecological relationship between the species and the relative values of the species. I shall henceforth refer to these as the *interdependence terms*.

3.6 Considering Species Interdependence

As before, three cases of species interdependence are considered: 1) independent species, 2) species competition, and 3) a predator-prey relationship.

3.6.1 Independent Species

In the independent case, each species' state equation is a function only of its own population and the land resource so that $G_1(x_1,x_2,L) = F_2(x_1,x_2,L) = 0$. Equations (3.10) and (3.11) become:

$$\dot{x}_1 = F(x_1,L) - h_1 \tag{3.33}$$

$$\dot{x}_2 = G(x_2,L) - h_2 . \tag{3.34}$$

Consequently, the interdependence terms of Equations (3.31) and (3.32) become zero, and the conditions revert to a pair of modified golden rule harvest conditions from the standard model.

$$\delta = F_1 - \frac{c_1'(x_1)F(x_1,L)}{R_1} \tag{3.35}$$

$$\delta = G_2 - \frac{c_2'(x_2)G(x_2,L)}{R_2} \tag{3.36}$$

In the independent species case, harvest decisions for each species are made without regard to the existence of the other species. In this respect, a two species model would yield the same results as two independently developed single species models if we failed to consider the constraint on returns to land. In a fisheries case, in which there are no returns to land to consider, species independence may be sufficient to justify the use of a single species model. However, for terrestrial conservation, each species is still dependent on the same land input for its production as indicated in Equation (3.30). Thus, both species still contribute to returns to the land resource even though each species may be harvested as indicated in a single species model. Swanson (1994) makes a compelling argument for considering returns to land in terrestrial species conservation. This model supports that argument and extends it by demonstrating the need to consider all relevant species in an ecosystem, even when they appear to be ecologically independent.

3.6.2 Competition

The distinguishing characteristic of this case is that each species acts against the interests of the other, so that $G_1(x_1,x_2,L)<0,\ F_2(x_1,x_2,L)<0$. Once again, the outcome is determined by the relative values of the species. If species 1 is of greater (lesser) value than species 2, then the magnitude of the term working against species 1 in Equation (3.31) is reduced (increased), and the magnitude of the term working against the second species in Equation (3.32) is increased (reduced). If competition exists between two species, the resource owner has the incentive to reduce populations of the lower value species, in favour of retaining the species with higher value. At moderate ratios of net revenue, the resource owner has insufficient incentive to exterminate the less valuable species, and populations of both species will be retained.

However, as one species gains significantly greater value than the other, the resource owner has an incentive to harvest the less valued species to extinction, so as to devote all of the land resources to production of the more valuable species. Livestock husbandry is the extreme manifestation of this behaviour.

3.6.3 Predator-Prey

The predator-prey relationship is defined as one in which the growth of one species is positively affected by the presence of the second, but in which the growth of the second species is adversely affected by the presence of the first. In the generalised model, this implies $G_1(x_1,x_2,L)<0,\ F_2(x_1,x_2,L)>0$ or $G_1(x_1,x_2,L)>0,\ F_2(x_1,x_2,L)<0$. Suppose species 1 is a predator ($G_1(x_1,x_2,L)<0$) and species 2 is its prey ($F_2(x_1,x_2,L)>0$). Then the interdependence term of

Equation (3.31) works against the predator (makes it less valuable), while the corresponding term in Equation (3.32), works in favour of the prey species. If both species have a harvest value, the predator, by reducing the growth of its prey, is reducing the potential returns to the land resource. Conversely, the prey is increasing potential returns by increasing the growth of the predator. The magnitudes of these impacts are dependent on the relative value of the two species. Two cases are offered: 1) the predator is of greater value than the prey and 2) the prey is of greater value than the predator.

(a) Predator has greater value ($R_1>R_2$).

As the value of the predator increases relative to that of the prey, the magnitude of the term working against the predator in Equation (3.31) is reduced, while the magnitude of the term working in favour of the prey in Equation (3.32) is increased. This creates a situation in which the relative values are working in favour of both species. At moderate ratios of net revenue, the resource owner has the incentive to maintain healthy positive populations of both species: the predator as a source of harvest revenue, the prey as a source of food for the predator and for harvest.

In the extreme case, as the net value of the prey approaches zero, Equation (3.31) reverts to something similar to the single species modified golden rule condition and Equation (3.32) approaches the (unmodified) golden rule. Interdependencies remain in these equations, however, as the predator is still dependent on the prey for food. The model predicts the relationship we would expect where a high-value predator is harvested and a low-value prey is not, in that significant populations of both stocks are maintained. The policy prescription for those wishing to conserve both species is clear: increase the value of the predator.

(b) Prey has greater value ($R_1<R_2$).

When the prey is of greater relative value, the magnitude of the term working against the predator in Equation (3.31) is increased, while simultaneously decreasing the magnitude of the term working in favour of the prey in Equation (3.32) (as the value of the prey as a food source for the predator is reduced). At modest ratios of net revenue, the owner has incentives to maintain both species, but at smaller equilibrium populations than when the predator has the greater value.

As the harvest value of the predator approaches zero ($R_1 \to 0$), given the prey has some positive net value ($R_2 > 0$), then the resource owner has the incentive to harvest the predator to extinction. This is the behaviour exhibited by livestock owners around the world as they seek to eliminate all predation of their stock, and is a principle cause of the decline of wild predators.

CHAPTER IV

DEVELOPING THE EMPIRICAL MODEL

4.1 Specifying Functional Form

The growth functions presented earlier require one crucial modification. Implicit in the earlier functions is the assumption that habitat available to the species in question is fixed. Given the role habitat loss plays in causing the decline of many wildlife species, this assumption is untenable. Alexander and Shields (2002), in their development of a bioeconomic model of New Zealand's Yellow-Eyed Penguin (*Megadyptes antipodes*), recognise this anomaly and suggest a further modification of the Verhulst logistic growth function as follows:

$$F(x) = \dot{x} = rx\left[1 - \frac{x}{K \cdot L}\right] \tag{4.1}$$

The additional variable, L, is added to the function given in Equation (3.1) to represent an index of suitable habitat available to the species. Adopting this approach, the parameter L is initially set at one to represent current land allocation. The term $K \cdot L$ can be viewed as the effective carrying capacity of the species habitat; as the size of land varies, so too does the effective carrying capacity.

It should be noted that specifying L in this manner assumes a linear relationship between the amount of land available and the carrying capacity of the habitat; that is, if land area is halved, so too is carrying capacity. When land allocation is altered dramatically, this relationship may not necessarily hold. For example, species that require large tracts of land, such as the African Wild Dog (*Lyacon pictus*), once a critical point is met, may experience far greater reductions in population than the corresponding loss of land would suggest. Nonetheless, for moderate variations in land allocation, this assumption seems reasonable.

Equations (3.3) and (3.4) can be adapted in a similar fashion, yielding:

$$\dot{x}_1 = r_1 x_1\left[1 - \frac{x_1}{K_1 \cdot L} + \alpha_{1,2}\frac{x_2}{K_1 \cdot L}\right] \tag{4.2}$$

$$\dot{x}_2 = r_2 x_2\left[1 - \frac{x_2}{K_2 \cdot L} + \alpha_{2,1}\frac{x_1}{K_2 \cdot L}\right] \tag{4.3}$$

In addition to the specification of a growth function, it is necessary to specify a cost of harvest function. Although there is an abundance of cost of harvest functions for marine species in the literature (see, for example, Conrad and Clark, 1987), little attention has been paid to the functional form of the cost of harvesting terrestrial species. This is no doubt due, at least in part, to the dearth of empirical terrestrial models.

Keeping in mind that our intention is to examine the economic implications of the single versus multiple species approach and not to produce a precise wildlife management tool (although this model should aid the development of such a tool), specification of the following Schaefer (1957) cost function seems appropriate:

$$c(x) = \frac{c_0 x_0}{x_t} \tag{4.4}$$

where $c(x)$ is the cost of harvesting an individual member of the species population,[12] c_0 is the initial cost of harvest, x_0 the initial stock level, and x_t the current stock level. Given an initial cost of harvest and stock level, a cost parameter C can be calculated, yielding the more familiar:

$$c(x) = \frac{C}{x_t} \tag{4.5}$$

The dynamics of this function are straightforward. As current stock levels rise, cost of harvesting an individual member of the species population falls. Conversely, as stocks tend to zero, cost of harvest tends to infinity.

With the introduction of functional forms as above, and reinstating time notation, the objective function and constraints for a *single* species model become:

$$\max_{h} \int_0^\infty e^{-\delta t} \left\{ \left[p - \frac{C}{x(t)} \right] h(t) - \delta p_L L(t) \right\} \tag{4.6}$$

The dynamics defining the stock of the species is represented by the state equation:

---

[12] In marine models this is usually the cost of harvesting a given mass (e.g. a tonne) of species stock, rather than the individual harvest cost.

$$\dot{x} = rx(t)\left[1 - \frac{x(t)}{KL(t)}\right] - h \tag{4.7}$$

For a *multiple* (two) species model, the objective function becomes:

$$\max_{h} \int_0^{\infty} e^{-\delta t} \left\{ \left[p_1 - \frac{C_1}{x_1(t)} \right] h_1(t) + \left[p_2 - \frac{C_2}{x_2(t)} \right] h_2(t) - \delta p_L L(t) \right\} \tag{4.8}$$

The dynamics defining the stock of each species are represented by the state equations:

$$\dot{x}_1 = r_1 x_1(t)\left[1 - \frac{x_1(t)}{K_1 L(t)} + \alpha_{1,2}\frac{x_2(t)}{K_1 L(t)}\right] - h_1 \tag{4.9}$$

$$\dot{x}_2 = r_2 x_2(t)\left[1 - \frac{x_2(t)}{K_2 L(t)} + \alpha_{2,1}\frac{x_1(t)}{K_2 L(t)}\right] - h_2 \tag{4.10}$$

4.2 Applying the Model

In this section, the model specified above is applied to three real-world examples (representing the three cases of species interdependence discussed earlier). The species chosen are all from the African Savannah, and the parameters chosen are representative of populations of those species within Kruger National Park.

Species independence is illustrated using the example of the African Elephant and the White Rhinoceros. The African Lion and the Blue Wildebeest serve as an example of predator-prey, while the Impala and the Greater Kudu illustrate interspecific competition.

4.2.1 Independent Species – The Case of the African Elephant and the White Rhinoceros

The plight of both the African Elephant and the White Rhinoceros is well documented. The ivory trade has reduced Elephant numbers from a population of nearly 1,700,000 in the late 1970s to less than 500,000 today (Barnes et al., 1999). Similarly, Rhinoceros horn, used as dagger handles and goblets in the Middle East and as traditional medicine in Asia, has been the principle agent of its decline. On a positive note, the White Rhinoceros stands as one of the world's greatest conservation success stories. From a population of just 20 in 1885, there are now nearly 10,000 Rhinoceros in the wild (Emslie and Brooks, 1999).

Nevertheless, both species remain vulnerable. The recent discovery of ten Elephant carcasses with tusks removed in the Tsavo East reserve in Kenya has sparked fears that the illegal ivory trade may be on the increase once again (Coates, 2002). In addition to poaching pressure, rapid growth of human population in Africa is putting these species into competition with humans for useable land, resulting in severe habitat loss. Although single species bioeconomic models of the Elephant exist (see, for example, Bulte and van Kooten, 1996), the facts that both species share a habitat, have considerable harvest value, and are often the focus of joint conservation efforts suggest there is a strong case for modelling the species together.

Available data suggest the intrinsic rates of growth (r) for Rhinoceros and Elephant are 9 percent and 6.5 percent respectively (Owen-Smith, 1988). Owen-Smith (1988) suggests that in favourable habitats, both Rhinoceros and Elephant are capable of reaching densities of 5 animals per square kilometre. Given that Kruger National Park covers approximately 2,000,000 hectares or the equivalent of 20,000 square kilometres, a figure of 100,000 serves as an estimate of carrying capacity (K).[13]

Harvest value (p) is calculated using information from African Safari Consultants (2002). Estimates are obtained by multiplying the per-person daily rate by the minimum number of days needed to hunt each particular species plus the appropriate trophy fee. This should be viewed as a conservative estimate. In many cases, the minimum number of days does not prove sufficient to guarantee a successful hunt for either of these species. The Elephant attracts a daily rate of \$650[14] for a minimum of ten days, plus a trophy fee of \$8,000, yielding a harvest value of \$14,500. The Rhinoceros attracts a daily rate of \$750, again for a minimum of ten days, plus a trophy fee of \$30,000, yielding a harvest value of \$37,500.

Determining the initial cost of harvest (c_0) is somewhat problematic. The overriding concern is to develop a method that allows the cost to be calculated in a consistent manner across all of the species in question. The method chosen is to calculate the initial cost of harvest as harvest value less the trophy fee. Although this should be

---

[13] For modelling purposes, all parameters (except discount and growth rates) are scaled by one thousand to enable the program to solve more easily. Before reporting all results are converted back to the appropriate scale.

[14] All figures are in US dollars.

considered an overestimate as a level of profit is undoubtedly built into the daily hunting rate, it allows the aforementioned concern to be met. This approach yields an initial cost of harvest of $6,500 for the Elephant and of $7,500 for the Rhinoceros.

Estimating an appropriate discount rate is fraught with controversy. A rate of 5 percent is chosen as the base case, representing a mid-point of the range found in the literature (Conrad and Clark, 1987; Bulte and van Kooten, 1996; Skonhoft, 1999). Due to the difficulty of estimating a universally acceptable discount rate, a sensitivity analysis is performed using a range of discount rates from 2 percent to 8 percent.

Hearne and Swart (2000) estimate the start-up cost of a typical game ranch to be $15,000 per square kilometre. Using this figure yields a land value for Kruger National Park of $300 million. This figure serves as an estimate of the value of land resource p_L.

The model is solved in discrete form for 150 periods using the General Algebraic Modeling System (GAMS). The GAMS command files for the models presented here can be found in the appendices. GAMS is specifically designed for modelling linear, non-linear and mixed integer optimisation problems. The non-linear programming solver CONOPT2 is used, as this is generally regarded the most suitable for this type of problem (GAMS, 1998). Whenever non-linear constraints are included, CONOPT2 solves a set of linearly constrained problems, recomputing linear approximations to the non-linear constraints at regular intervals. Since CONOPT2 solves the problem in this way, it is necessary to set starting values of variables to provide points around which initial linear approximations can be computed. If no starting values of variables are specified, GAMS sets all variables equal to zero. This frequently implies that some or all of the partial derivatives are also equal to zero. In this case, some or all of the constraints are approximated either with non-existent functions or functions with an empty solution set (Brooke, et al., 1992).

For all models, the starting stock value is set as the actual stock level of the species in question, obtained from the Kruger National Park year 2000 census (ECOAFRICA, 2002). For Elephants and Rhinoceros this implies starting values of 9,152 and 2,500 respectively. Initial harvest rates are set relatively low at 100 in order to reduce the probability of initial harvest dramatically reducing stocks, which would necessarily have ongoing ramifications for future periods.

Since non-linear equations may be undefined (or unrealistic) at certain values of the endogenous variables, it is also necessary to restrict the domains of variables through the imposition of upper and lower bounds. In all cases, bounds are set as wide as necessary to ensure (realistic) optimal solutions are found before bounds are reached. The societal objective function and constraints are defined for the single species model by Equations (4.6) and (4.7), and for the multiple species model by Equations (4.8), (4.9) and (4.10).

In seeking to reflect the fact that wildlife species are more likely to be facing net loss (as opposed to net gain) of habitat in the foreseeable future, land is given an upper bound of 1.0 (current allocation), with any value below this point representing a scenario whereby further habitat loss is likely. If such a bound is not set, the model simply varies land allocation period by period as needed, so that when stocks are high, land allocation rises, and when stocks are low, land allocation falls. This is clearly an unrealistic outcome; the opportunity for wildlife managers to vary land allocations in this manner is limited.

The first results presented (Figure 4.1, p.65) are the optimal stock levels of the African Elephant under a single and a multiple species model; the command files for these models are given in Appendices A and C. The single species result suggests that the harvesting of Elephants alone generates an insufficient return to ensure the survival of the species. The model predicts an immediate harvest of Elephants back to 5 percent of initial density (from an initial stock of 9,152 to 540), and thereafter harvesting to keep numbers at this level. The continued presence of Elephants (albeit at critically low levels) probably owes more to the specification of a cost function, which makes harvesting small populations prohibitively expensive, than to the value derived from the Elephants themselves. This result can therefore be regarded as predicting the extinction of Elephants.

In contrast, the inclusion of the more valuable Rhinoceros (in the multiple species case) affords the Elephant access to the resources necessary for its continued survival, with periodic harvesting approximately every 30 periods. This keeps the

Elephant within a stock limit cycle in the order of half to three and half times initial density (a stock range of 4,500 to 31,200).

In effect, the value generated from the continued existence and harvest of the Rhinoceros subsidises continued existence and harvest of the Elephant. This result underlines the potential for misapplication of single species results and, illustrates the importance of considering all species of value in management decisions, even in the absence of any direct ecological relationship.

Figure 4.2 (p.65) presents the optimal stock levels of the White Rhinoceros under a single and a multiple species model; the command files for these models are given in Appendices B and C. As the high-value species, the stock level of the Rhinoceros is relatively unaffected by the presence of the Elephant in the model, although the multiple species case generates a more stable long-run stock and harvest level, with a fractionally larger average harvest over the time period in question. This result arises from the relationship shown in Equation (3.30), which acts to 'charge' each species for the entire value of the land in the single species case, but which allows them to share the burden in the multiple species situation.

The oscillating level of stock seen in the single species case of Figure 4.2 is a common result when logistic growth functions of the type specified here are solved in discrete time. As the intrinsic growth rate (r) rises, the population size tends to vary in a wholly irregular, non-periodic manner with different outcomes resulting from different starting values. This behaviour is referred to as dynamic 'chaos' (Conrad and Clark, 1987).

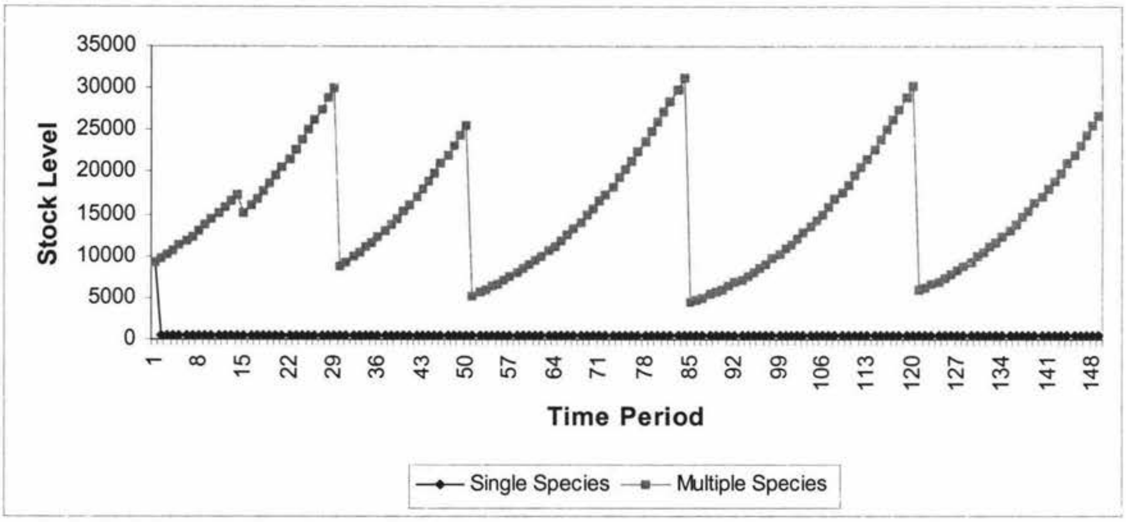

Figure 4.1: Optimal Stock Levels for the African Elephant under a Single and a Multiple Species Model

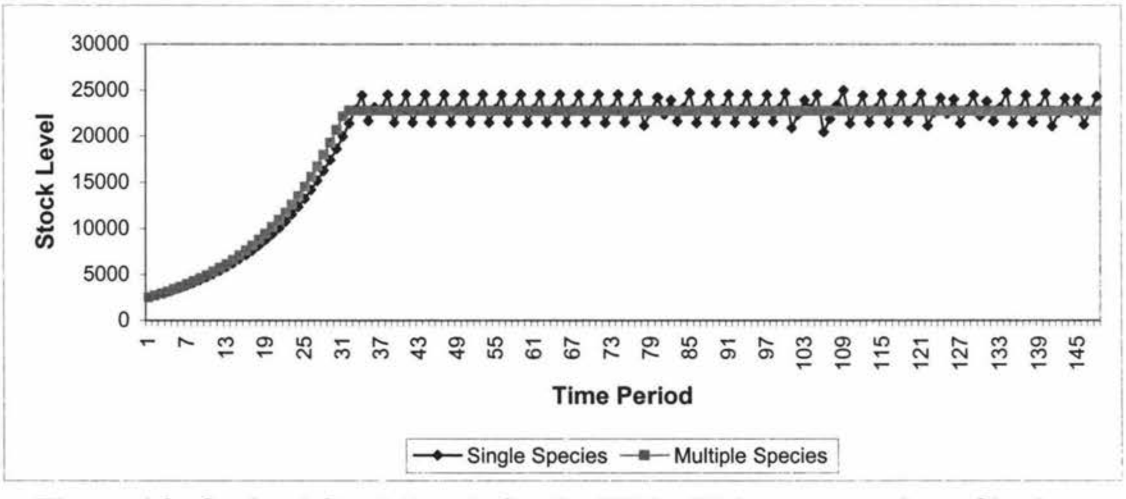

Figure 4.2: Optimal Stock Levels for the White Rhinoceros under a Single and a Multiple Species Model

Optimal land resource allocation under a single species Elephant, a single species Rhinoceros and a multiple species model is presented in Figure 4.3 (p.66); the command files are given in Appendices A, B and C. The high value Rhinoceros generates sufficient return in the long-run to allow the initial allocation of land resources to continue, although the multiple species case, with the addition of revenue from the Elephant, is able to provide this return more quickly. The Elephant alone, however, is unable to generate sufficient return to justify the continued allocation of land resource, and it is this, not the value of the harvested products per se, which motivates the harvesting decision discussed above.

This result has clear implications for the use of single species versus multiple species models. In this case, a single species model of the Elephant would suggest that conversion of land resources currently devoted to Elephant habitat is the appropriate response, given the incentives faced. With the addition of the Rhinoceros, land conversion becomes sub-optimal, with habitat best remaining in its current use.

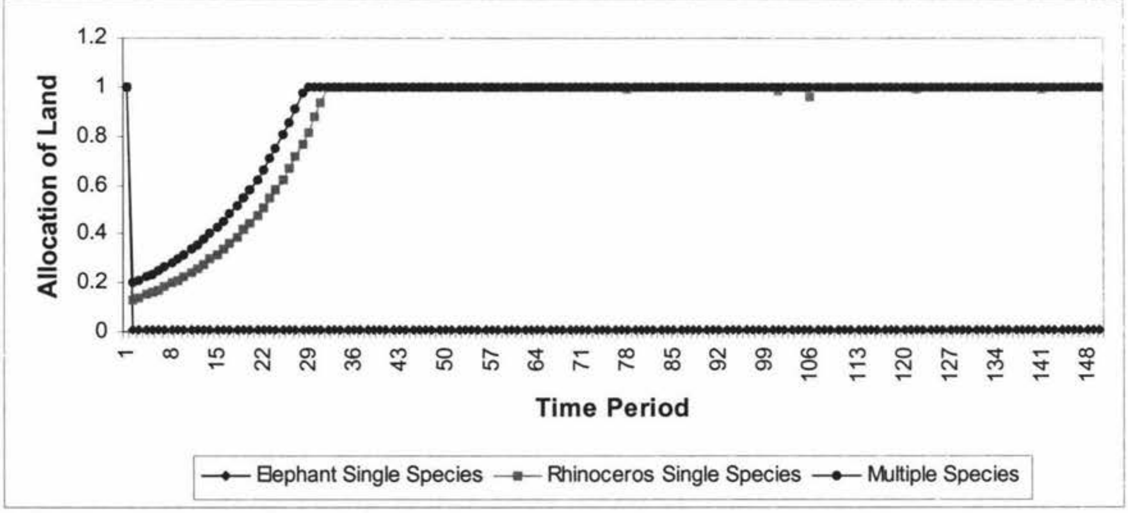

Figure 4.3: Optimal Land Resource Allocation to the African Elephant and White Rhinoceros under a Single and a Multiple Species Model

As discussed above, a sensitivity analysis is performed to explore the implications of specifying an alternative discount rate. Results for a discount rate of 6.5 percent, 5 percent (the base case) and 3.5 percent are presented in Figures 4.4 and 4.5 (p.68). The base model command files are given in Appendix C; the sensitivity analysis is performed through varying the scalar discount rate, and the discount factor. Figure 4.4 presents the effect of altering the discount rate on the optimal stock level of the

Elephant under a multiple species model. As we would expect, a high discount rate (opportunity cost of capital (land)) corresponds to a lower mean Elephant stock, which in turn means that harvesting becomes heavier but less frequent. Specifically at a discount rate of 6.5 percent, harvesting occurs on average every 50 years, at which time stocks are reduced to approximately 5 percent of their pre-harvest density. Again, the continued presence of Elephants is probably owed to the specified cost function. The mean stock level over the period is less than 6,000. It should be noted that once the discount rate reaches double figures, even with the Rhinoceros' 'subsidy', Elephants are immediately harvested to critically low levels, and thereafter harvested to keep numbers at this level.

In contrast, at a discount rate of 3.5 percent, harvesting occurs on a regular 17-year cycle, each event reducing stock by 50 percent. This produces a mean stock level over the period in excess of 25,000 and, although the mean harvest of approximately 19,500 is lower than the mean harvests at a higher discount rate, the total harvest is significantly higher with in excess of 136,000 Elephants harvested over the 150-year period, compared with less than 90,000 being harvested in the base case.

The effect of altering the discount rate on the allocation of land is presented in Figure 4.5. Although at all discount rates within the tested bounds of 2 to 8 percent the model predicts the current allocation of land to remain, the speed at which the model reaches this allocation differs. Essentially, and unsurprisingly, as the discount rate and therefore the opportunity cost of land increases, the more slowly the model predicts a return to the current allocation. Specifically, at a discount rate of 6.5 percent, optimal land allocation takes 27 periods to reach current levels. This compares with the base rate where current levels are reached in 22 periods and a rate of 3.5 percent, where this allocation is reached in 17 periods.

The high net value of the Rhinoceros makes it impervious to changes in the discount rate, and hence this result is not reported.

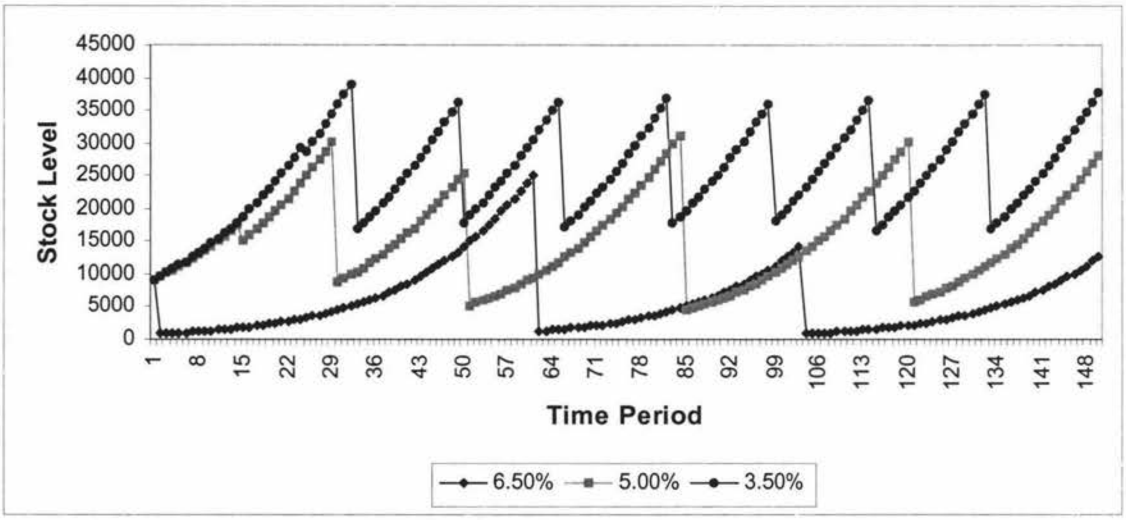

Figure 4.4: Optimal Stock Levels for the African Elephant under a Multiple Species Model with Alternative Discount Rates

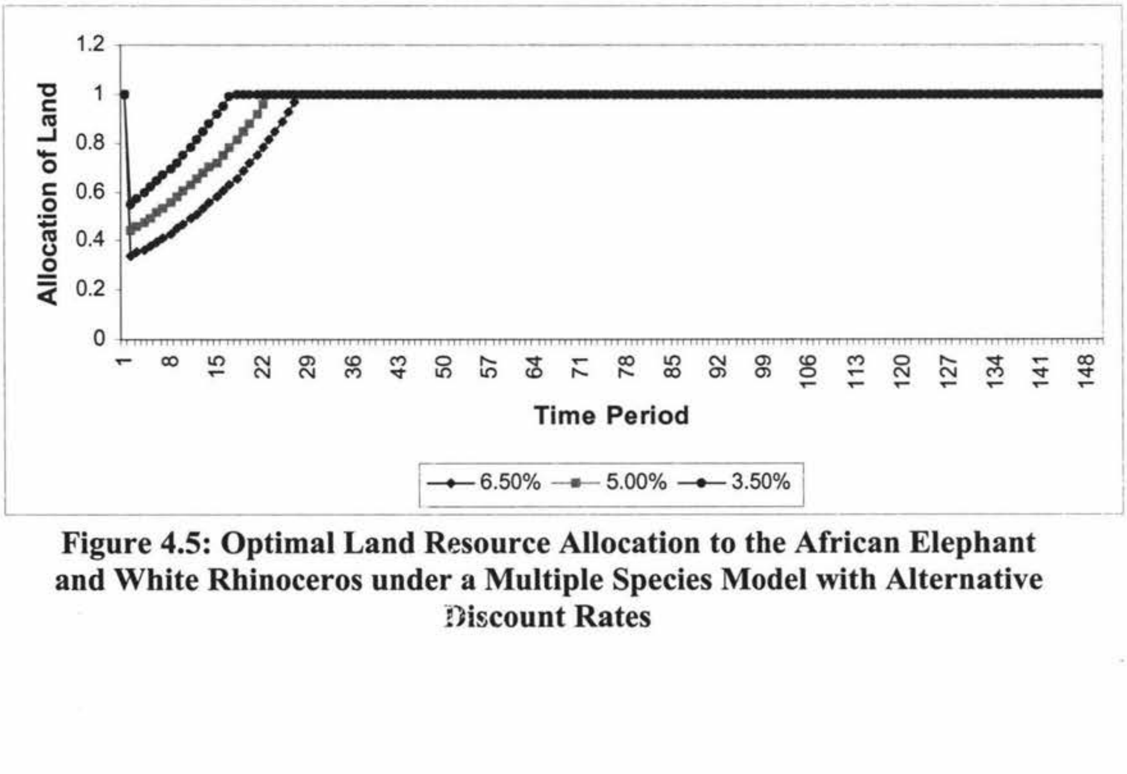

Figure 4.5: Optimal Land Resource Allocation to the African Elephant and White Rhinoceros under a Multiple Species Model with Alternative Discount Rates

4.2.2 Interspecific Competition – The Case of the Impala and Greater Kudu

Impala are among the most numerous mammal species in southern Africa. Kruger National Park alone has an estimated Impala stock of 100,000, and the Impala is numerically the most important single species available for game hunting in the majority of the region's game ranches (Fairall, 1982).

Whereas the Impala, with its high rate of growth and carrying capacity, has become a favourite of the burgeoning game ranch industry, Kudu remains conservation dependent. In southern Africa, Kudu have been hunted for many years, the meat is highly valued and the horns of the male Kudu are a trophy for many game hunters. Natural jumpers, Kudu prefer lower densities than the Impala. While more valuable, they are more difficult to manage, especially on smaller ranches. Both species favour a similar habitat; Impala are mixed grazer-browsers while Kudu are browsers. Evidence suggests a degree of competition between the two, especially in times of drought (Huffman, 2002).

Data suggests the intrinsic rates of growth (r) for Impala and Kudu are 35 percent and 20 percent respectively. In favourable habitat, Impala are able to reach considerable densities of up to 20 animals per square kilometre, while Kudu are able to reach densities of up to 15 animals per square kilometre (Falkena, 2000). These figures yield, for Kruger National Park, carrying capacities of 400,000 and 300,000 for Impala and Kudu respectively.

A harvest value (p) and initial cost of harvest (c_0) for both species is calculated in a manner similar to that of the Elephant and the Rhinoceros. Plains game hunting is charged at a daily rate of \$350 with no specified minimum days. Impala attract a trophy fee of \$250, yielding a harvest value (based on a single day's hunting) of \$600. Kudu attract a trophy fee of \$1000, yielding a harvest value of \$13,500. Again this should be viewed as conservative.

As before, initial cost of harvest is calculated to be harvest rate less trophy fee, yielding \$350 for both species. The observation made on the estimate of initial cost of harvest for the Elephant and Rhinoceros, namely that cost should be considered inflated, is equally applicable in this case.

As with Elephant and Rhinoceros, initial stock levels are set at the actual stock level obtained for the Kruger National Park year 2000 census. This yields initial stock levels of 100,000 and 3,500 for Impala and Kudu respectively (ECOAFRICA, 2002). As discussed in Chapter 3 earlier, interaction coefficients $\alpha_{1,2}$ and $\alpha_{2,1}$, if competitive coexistence is to be possible, must be bounded. Specifically, $\alpha_{1,2} < \frac{K_1}{K_2}$ and $\alpha_{2,1} < \frac{K_2}{K_1}$. In this case, the implication is that $\alpha_{1,2}$ must be less than 1.33 and $\alpha_{2,1}$ must be less than 0.75. The approach taken is to take the midpoint of each bound, giving an $\alpha_{1,2}$ of 0.665 and an $\alpha_{2,1}$ of 0.375. Recognising that this is a somewhat arbitrary approach, sensitivity analysis at the lower and upper quartile of each bound is undertaken to explore the implications of using alternative interaction coefficients.

In order to generate meaningful stock and harvest dynamics, given the relatively low harvest values of each species, it is necessary to adjust the value of the land resource parameter. If left at \$15,000 per square kilometre, the model simply harvests both species to extinction in the first period. Impala and Kudu themselves do not generate sufficient return to justify the continued use of the valuable land resource, a predictable result that reinforces the necessity of taking into account the value of all relevant species in this type of model. Accordingly, p_L is taken to be \$1,500 per square kilometre in order to observe the interaction dynamics between the species. As the purpose of the model is to investigate the variations inherent in single versus multiple species models, the arbitrary adjustment of land values should not adversely affect our results. As the primary effect of adjusting the discount rate is to alter the opportunity cost of land, and land is given an artificially low value in this model, there is little to be gained from performing a sensitivity analysis on this parameter. All other parameters are consistent with the earlier models.

The optimal stock levels of Impala under a single and a multiple species model are presented in Figure 4.6 (p.72); the command files are given in Appendices D and F. The effect of interspecific competition is clear: Impala's multiple species steady-state stock level falls below the bounds of the oscillating single species levels. Specifically, under a single species model, the Impala stock level oscillates between a population bound of 145,000 to 185,000, with harvesting on a regular basis. As with the Rhinoceros, the oscillating pattern can be attributed to the specification of a logistic growth function, coupled with a high intrinsic growth rate.

Under a multiple species model optimal stocks of Impala (that are now competing with Kudu for scarce resource) are consistently lower, at a stable stock level of approximately 135,000. Harvest levels are simply kept at a level sufficient to maintain this long-run stable population.

The optimal stock levels of Kudu are presented in Figure 4.7 (p.72); the command files are given in Appendices E and F. Under a single species model Kudu reach an optimal long-run steady-state population of approximately 118,000 with harvesting to keep the population at this level. With the introduction of a competitor, namely the Impala, the long-run steady-state population falls to approximately 88,000, and harvesting falls accordingly to keep the population at this reduced level. In sum, the multiple species result produces a lower stock and harvest level for both competing species.

A sensitivity analysis is performed, seeking to explore the implications of altering the interaction coefficients. The method employed is to hold one of the interaction coefficients constant and vary the other. The case where Kudu have a greater (than the base case) impact on Impala $(\alpha_{1,2} > 0.665)$ yields lower stock levels of Impala, an intuitive result. However, when Impala have a greater (than the base case) impact on the Kudu $(\alpha_{2,1} > 0.375)$ *Impala* stocks are lower. This result is not as immediately intuitive.

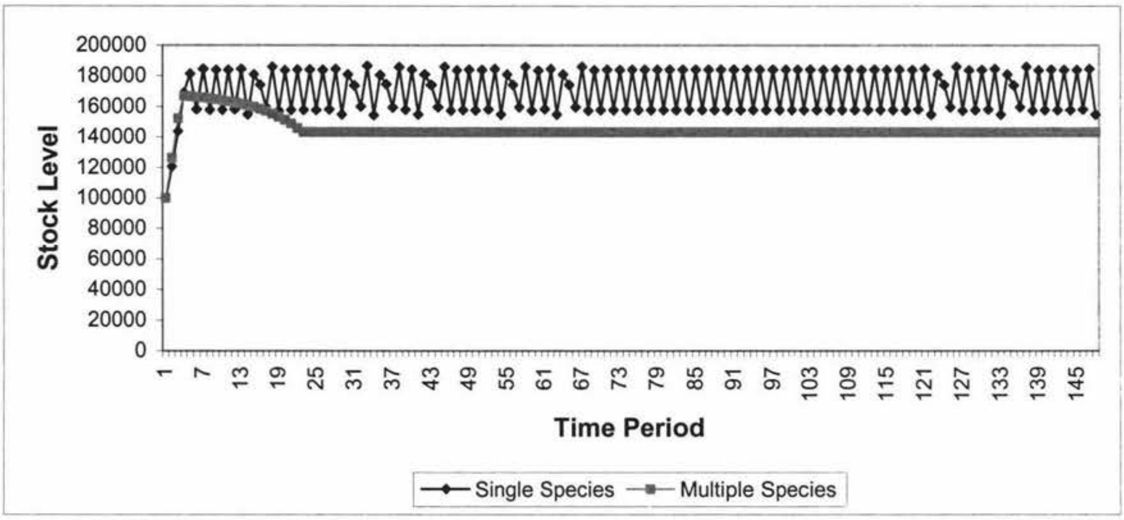

Figure 4.6: Optimal Stock Levels for the Impala under a Single and a Multiple Species Model

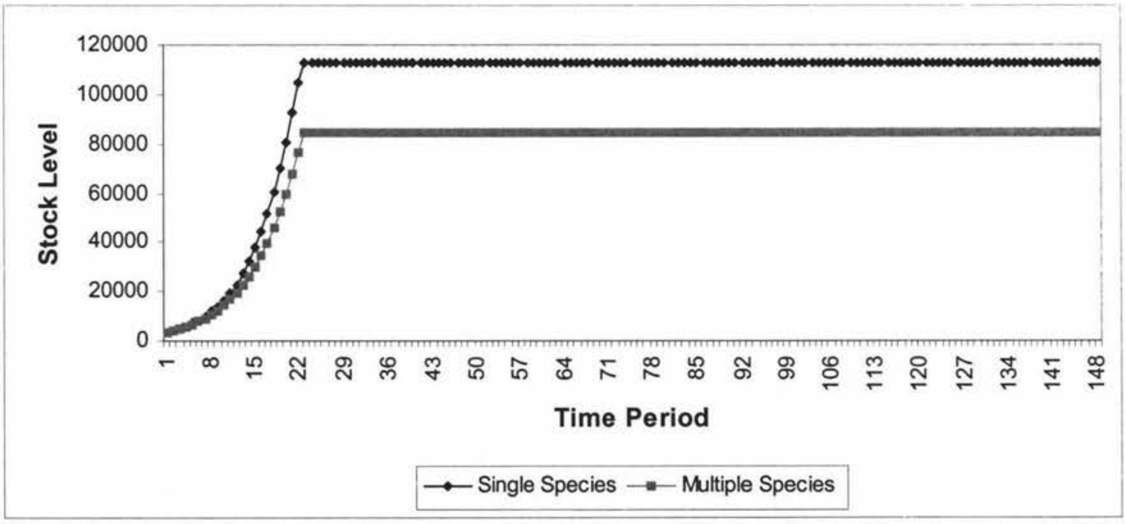

Figure 4.7: Optimal Stock Levels for the Greater Kudu under a Single and a Multiple Species Model

The case where $\alpha_{1,2}$ is held at the base case $(\alpha_{1,2} = 0.665)$ and $\alpha_{2,1}$ is varied is presented in Figure 4.8 (p.73). The base model command file is given in Appendix F; the sensitivity analysis is performed through varying the interaction coefficient - scalar a2. As previously discussed $\alpha_{2,1}$ is bound between zero and 0.75, Figure 4.8 presents the midpoint of this bound $(\alpha_{2,1} = 0.375)$, the lower quartile $(\alpha_{2,1} = 0.1875)$ and the upper quartile $(\alpha_{2,1} = 0.5625)$. As illustrated, although the stock level trends are similar between the three cases, the greater the impact of Impala on Kudu, the lower the steady-state stock level of Impala. Unlike the alternate case (where $\alpha_{1,2}$ is varied) the economic, rather than the ecological relationship is the primary driving force of this result. The lower stock level seen in the presence of a greater $\alpha_{2,1}$ is not a result of dampened growth ($\alpha_{2,1}$ does not enter the Impala's growth function), but is a result of a harvesting regime seeking to protect the growth rate of the more valuable Kudu from the dampening effects of Impala. This result is reinforced by the sensitivity analysis (not reported) that found the effects on Kudu populations of varying $\alpha_{1,2}$ (the effect of Kudu on Impala) to be negligible.

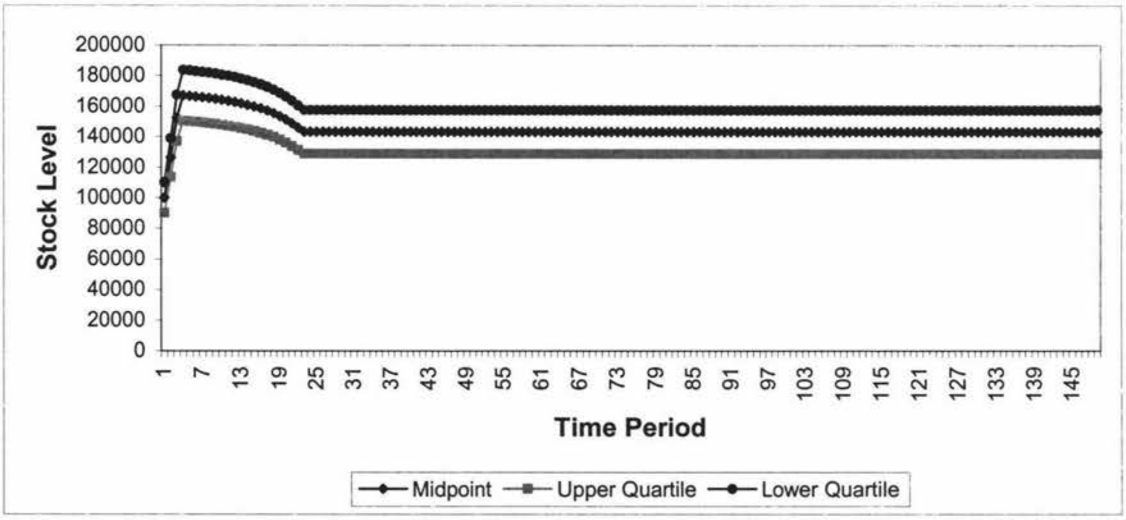

Figure 4.8: Optimal Stock Levels for the Impala under a Multiple Species Model with Alternative Interaction Coefficients

Under the unrealistic land value specified, the Impala and the Kudu alone and as a pair are capable of retaining use of their land at the initial level. As aforementioned, this result does not hold if the true opportunity cost of land is considered, making reporting the dynamics of land allocation of little value.

4.2.3 Predator – Prey Species – The Case of the African Lion and the Blue Wildebeest

The Lion is the largest of all African carnivores and is one of the most charismatic and revered species to inhabit the African Savannah. The distribution range of the Lion has shrunk considerably in historic times. It became extinct in Europe some 2,000 years ago and disappeared from northern Africa and most of southwest Asia 150 years ago. In the wild outside of Africa today, only a remnant population numbering about 250 of the sub-species *Panthero leo persica* (the Asiatic Lion) survives in the Gir Forest of India. At the beginning of the twentieth century the Lion was found in all suitable habitat throughout Africa south of the Sahara. However, there too it is becoming increasingly rare outside large conservation areas. In Western Africa numbers are reported to have fallen drastically and Lions are now mainly confined to the larger conservation areas. It is on the perimeter of these that most conflict occurs (African Lion Working Group, 2000).

The IUCN status of the Lion is considered to be 'Vulnerable'. Not surprisingly, Lions are generally considered serious problem animals whose existence is at odds with human settlement and stock husbandry. Cattle farmers see Lions as a threat to stock and are known to shoot them. As scavengers, Lions will pick up poisoned meat, often meant for other predators (IUCN, 2000).

The most common medium-sized to large herbivores in different ecosystems make up the bulk of the Lion's diet. In Kruger National Park Wildebeest form a significant component of the Lion's diet and Lion predation acts as a limiting force on their population (Schaller, 1972).

The Blue Wildebeest, also known as the Brindled Gnu, is one of the most common bushveld species in southern Africa. They are found in Botswana, South Africa, Namibia, and Zimbabwe. They are categorised as lower risk, conservation dependent by the IUCN, a reflection of increasing pressure on their habitat from humans. They are social creatures and live in groups of 20 to 40 animals, sometimes in larger herds, the members of which are usually cows and calves, led by a bull. Being essentially grazers, Wildebeest show preference for open savannah woodland and open grassland and access to drinking water is essential (Planet Wildebeest, 1997).

Data suggests the intrinsic rate of growth (r) for the Lion and Wildebeest are 11 percent and 25 percent respectively. In the presence of sufficient prey Lions are able to reach densities of up to 5 animals per square kilometre, while Wildebeest are able to reach densities of up to 10 animals per square kilometre (Schaller, 1972; Planet Wildebeest, 1997). These figures yield a carrying capacity (K) for Kruger National Park of 100,000 and 200,000 for Lion and Wildebeest respectively.

A harvest value (p) for both species is calculated in a manner similar to previous models. Hunting for Lion attracts a daily rate of $650 for a minimum of ten days. Trophy fees varies widely, dependent upon whether a Lion or Lioness is killed. Data on recent trophy fees suggests that kills are evenly divided between the two, and therefore an average of the two is taken. This, together with the cost of hunting, yields a total harvest value of $13,500. Wildebeest attract a trophy fee of $800, which, together with the cost of a single day's plains game hunting, yields a harvest value of $1,150. Cost of harvest is again determined to be harvest value less trophy fee. Observations made about the estimates of price and cost of harvest for previous models are again applicable (African Safari Consultants, 2002). Initial stock levels are again set at the actual stock level, obtained from the Kruger National Park year 2000 census, yielding initial stock levels of 2,500 and 14,000 for the Lion and Wildebeest respectively (ECOAFRICA, 2002).

As discussed in Chapter 3 earlier, interaction coefficients $\alpha_{1,2}$ and $\alpha_{2,1}$, if positive stocks of predator and prey are to be possible, must be bounded. Specifically, $\alpha_{1,2} < \frac{K_1}{K_2}$ and $\alpha_{2,1} < \frac{K_2}{K_1}$. The implication in this case is that $\alpha_{1,2}$ must be less than 0.5 and $\alpha_{2,1}$ must be less than 2.00. Again, the midpoints of these bounds serve as the base case. As with the competitive case, a sensitivity analysis is performed to explore the implications of using alternative interaction coefficients. It is again necessary to adjust the value of the land resource parameter to generate meaningful stock and harvest dynamics. Lion and Wildebeest themselves do not generate sufficient return to justify the continued use of the valuable land resource. For consistency, p_L is taken to be $1,500 per square kilometre. All other parameters are consistent with the earlier models.

The optimal stock levels of the Lion under a single and a multiple species model are presented in Figure 4.9 (p.76); the command files are given in Appendices G and I. Under a single species model, Lion populations oscillate between 21,000 and 32,000 on a regular six-year cycle. In contrast, with the inclusion of Lion's predatory effect on Wildebeest, the multiple species model produces an initial surge in population, followed by a period of rapid decline, with stock levels reaching single figures in the 88th period. This result can be viewed as predicting extinction for the Lion. This is of interest, in that although a single Lion is of significantly greater value than a single Wildebeest, the size of the Wildebeest population, coupled with the ability of it to grow (and therefore be sustainably harvested) at over twice the rate of the Lion, serves to make the Wildebeest the more attractive option.

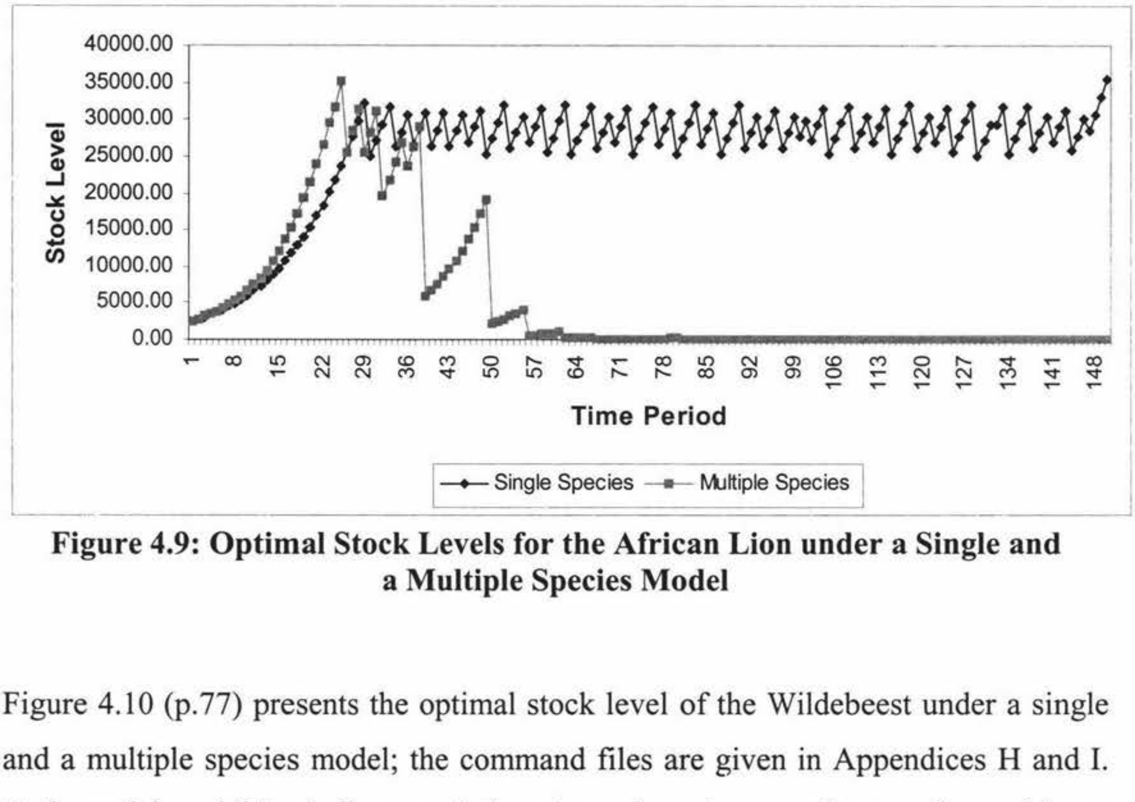

Figure 4.9: Optimal Stock Levels for the African Lion under a Single and a Multiple Species Model

Figure 4.10 (p.77) presents the optimal stock level of the Wildebeest under a single and a multiple species model; the command files are given in Appendices H and I. Both models exhibit similar population dynamics, strong early growth reaching a steady-state stock level. The single species result reaches a long-run steady-state level of approximately 80,000 with annual harvesting of 12,000 animals to maintain populations at this level. The multiple species model initially overshoots the long-run steady-state level of 100,000 with populations reduced to the steady-state level through a combination of heavy harvesting and Lion predation (as Lion populations are strong at this time). The fact that Wildebeest obtain a higher long-run steady-state level when Lions are present is a result of their value as prey (in addition to their harvestable value) for the remaining Lion population. This result concurs with Strobele and Wacker (1995) who, for the case of a marine predator-prey system, conclude that the optimal stock of prey is always greater under a multiple species framework, than when modelled alone.

To determine whether reducing the Lion's predatory impact on Wildebeest would reduce the incentive to harvest the Lion to virtual extinction, the interaction coefficient ($\alpha_{2,1}$) is altered. The results for the base line (midpoint) case where $\alpha_{2,1}$ is 1.0, the upper quartile where $\alpha_{2,1}$ is 1.5 and the lower quartile where $\alpha_{2,1}$ is 0.5 are given in Figure 4.11 (p.78). The base model command file is given in Appendix I, variations are made to the interaction coefficient - scalar a2. The effect of these adjustments is to alter the time it takes for Lion populations to be driven to unsustainable levels - the greater the predatory impact the Lion has on the Wildebeest (higher $\alpha_{2,1}$), the sooner these levels are reached. Clearly it is the predatory effect of the Lion that is the cause of its decline, rather than its lack of harvestable value, a result reinforced by the strongly positive stock levels produced in the single species model.

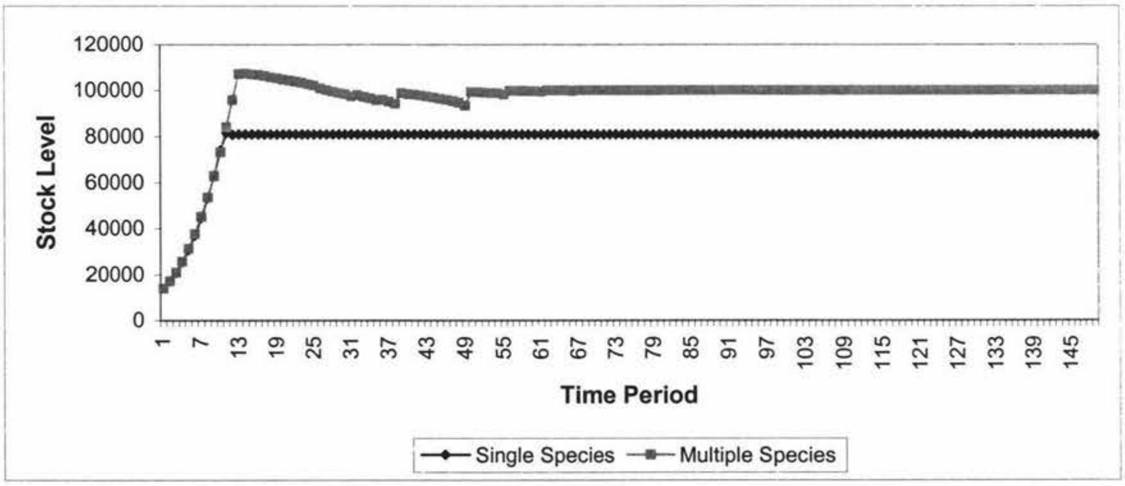

Figure 4.10: Optimal Stock Levels for the Blue Wildebeest under a Single and a Multiple Species Model

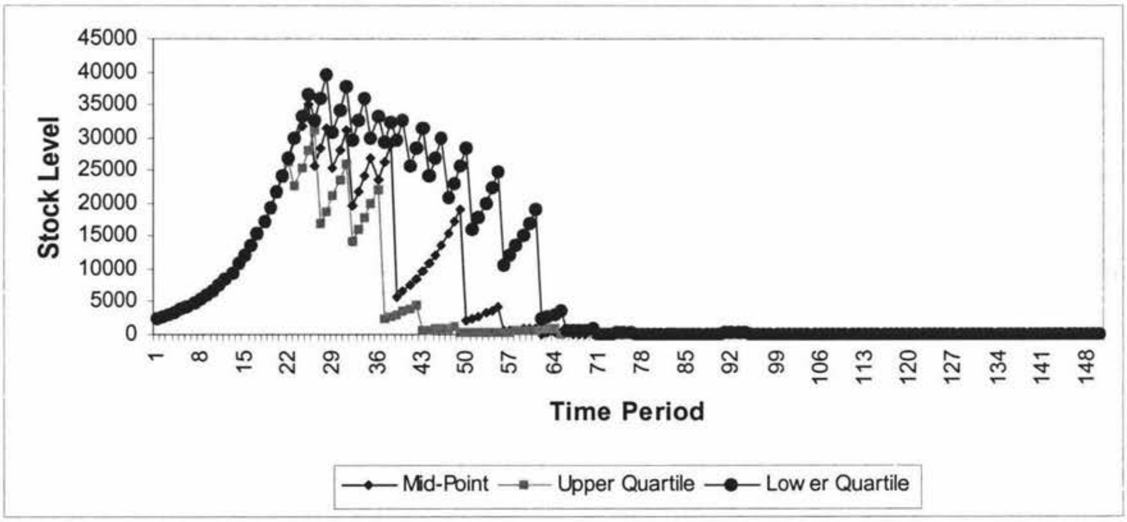

Figure 4.11: Optimal Stock Levels for the African Lion under a Multiple Species Model with Alternative Interaction Coefficients

CHAPTER V

SUMMARY AND CONCLUSIONS

5.1 Summary

5.1.1 Introduction

Conservation efforts have traditionally focused on the identification and preservation of a small number of charismatic species. This approach has increasingly been challenged as our knowledge of the many and varied interactions among species, their habitat, and the environment has improved. While the ecological implications of modelling species in isolation rather than as part of an ecosystem are well documented (Pimm, 1991; Begon et al., 1996; Milner-Guilland and Mace, 1998), little attention has been paid to the economic implications. This thesis seeks to redress this imbalance by exploring the introduction of multiple species into the traditional bioeconomic framework.

The bioeconomic modelling of species extinction has grown out of the literature of fisheries economics. Working from Gordon's (1954) seminal fisheries model, Clark (1973) develops a model to analyse the decision-making of a sole owner seeking to maximise the present value of his harvests. He identifies the conditions under which the owner has an economic incentive to harvest the species to extinction. Clark identifies three conditions that would make such a choice 'optimal'. These are 1) open-access to the resource; 2) price-to-cost ratio of harvesting the resource greater than one; and 3) low growth rate of the resource relative to the social discount rate. If either the first condition or the last two conditions are met, then resource extinction can occur.

Many extensions have been made to Clark's original model. Swanson (1994), recognising that, unlike marine species, terrestrial species compete with humans for the use of land resources, seeks to bring the literature 'onshore' by including land resources as an additional control variable.

A notable feature of the extensions to Clark's original model is their single species focus. Although many authors acknowledge the shortcomings of such an approach (Ragozin and Brown, 1985; Bulte and van Kooten, 1996), the bioeconomic literature remains dominated by single species models.

The single and multiple species results of terrestrial bioeconomic models are compared, paying particular attention to the potential consequences of misapplying a single species model to a multiple species situation. Three cases of species interaction are considered: ecological independence, predator-prey interaction and interspecific competition.

5.1.2 Developing the Model

The growth function in a bioeconomic model can be considered to be analogous to the production function in general economic theory. Production economics literature makes clear the distinction between firms producing single outputs and those producing multiple outputs (Beattie and Taylor, 1985). A single species model clearly assumes the former to be the case. However, to the extent that the allocation of land resources for conservation of one species necessarily provides habitat to other species which share that land, conservation management may be more properly viewed as a multiple product production process.

A simple two species model is developed to demonstrate the effect of adding additional species to the single species bioeconomic framework. Assuming society wishes to maximise the present value of net returns from harvesting both species, the following objective function is specified:

$$\max_{h} \int_{0}^{\infty} e^{-\delta t}\{[p_1 - c_1(x_1)]h_1 + [p_2 - c_2(x_2)]h_2 - \delta p_L L\} \tag{5.1}$$

where subscripts denote species 1 and 2, L is a unit of terrestrial resource (land) upon which the species depends for survival, and p_L is the unit price of a base unit of that land resource.

The dynamics defining the stock of each species are represented by the state equations:

$$\dot{x}_1 = F(x_1, x_2, L) - h_1 \tag{5.2}$$

$$\dot{x}_2 = G(x_1, x_2, L) - h_2 \tag{5.3}$$

where $F\left(x_1,x_2,L\right)$ and $G\left(x_1,x_2,L\right)$ are the joint production functions of species 1 and 2, where the land resource, L, is non-allocable.[15]

Using the Pontryagin necessary conditions for maximisation of this problem and simplifying the notation by allowing $R_1 = R_1(x_1) = p_1 - c_1(x_1)$ and $R_2 = R_2(x_2) = p_2 - c_2(x_2)$ to represent net revenues from harvest, the following conditions are derived:

$$\delta = \frac{R_1 F_L}{p_L} + \frac{R_2 G_L}{p_L} \tag{5.4}$$

$$\delta = F_1(x_1,x_2,L) - \frac{c_1'(x_1)F(x_1,x_2,L)}{R_1} + \frac{R_2}{R_1}G_1(x_1,x_2,L) \tag{5.5}$$

$$\delta = G_2(x_1,x_2,L) - \frac{c_2'(x_2)G(x_1,x_2,L)}{R_2} + \frac{R_1}{R_2}F_2(x_1,x_2,L) \tag{5.6}$$

We assume throughout that $R_1, R_2 > 0$ for all relevant levels of x_1, x_2, otherwise the cost of harvest would exceed the revenues and no harvest would occur. Equation (5.4) reflects the impact of the land control term in the objective function and is a multiple species version of the result found by Swanson (1994). This condition implies that society will allocate land only to the extent that the species supported by it are able to generate a competitive rate of return from their use of the resource. In a single species model, it would appear that this return must be generated entirely by the species under consideration. However, when the conservation of a wilderness area provides benefits to many species, the returns generated by all species may contribute to meeting the required returns from the land resource.

Equations (5.5) and (5.6) are modified golden rule equations for species 1 and 2 respectively. The LHS and the first term on the RHS indicate that the resource must be maintained at a stock level such that the marginal productivities of the resource stocks, F_1 and G_2, equate to the return available from other assets, δ. All other terms on the RHS modify that relationship.

The second terms on the RHS of Equations (5.5) and (5.6) reflect the stock-dependent harvest costs ($c'(x) < 0$), expressed proportionately to the unit net revenue

---

[15] A non-allocable factor of production is one for which the amount of it used in producing a given output y_1 cannot be distinguished from the amount of that factor used in producing output y_2 (Beattie and Taylor, 1985).

of harvesting the resource. The only adjustment from the single species case is that the growth functions, $F(x_1, x_2, L)$ and $G(x_1, x_2, L)$, are now potentially interdependent. As before, this term acts to increase the marginal productivity of the resource, making the resource a more attractive investment. While these terms exhibit potential interdependence between species, they arise directly from the harvest activity and are strongly dependent on the ratio of marginal costs to marginal revenues.

The third terms on the RHS of Equations (5.5) and (5.6) reflect the biological interdependence of the two species, modified by the relative marginal profitability of each. Each equation indicates that returns for one species are modified by the marginal affect that the species has on the other, times the proportional revenue of the other species to the first. Whether this makes a species more or less desirable in the human asset portfolio depends upon both the ecological relationship between the species and the relative values of the species. These are referred to as the *interdependence terms*.

Three cases of species interdependence are considered: 1) independent species, 2) a predator-prey relationship and 3) species competition.

In the independent case, each species' state equation is a function only of its own population and the land resource. Consequently, the interdependence terms of Equations (5.5) and (5.6) become zero, and the conditions revert to a pair of modified golden rule harvest conditions from a standard single species model.

With independent species, the only condition that still varies from the standard single species bioeconomic model is Equation (5.4). Thus, both species still contribute to returns to the land resource but each species is harvested in exactly the manner they would be in a single species model.

The distinguishing characteristic of the competitive case is that each species acts against the financial interest of the other. Here we have the situation where the outcome is determined by the relative values of the species. If species 1 is of greater (lesser) value than species 2, then the magnitude of the term working against species 1 in Equation (5.5) is reduced (raised), and the magnitude of the term working against the second species in Equation (5.6) is increased (reduced). If competition exists between two species, the resource owner has the incentive to harvest the low value species in favour of retaining the species with high value. In the presence of strong competition, when one species is of significantly greater value than the other, the resource owner has the incentive to harvest the unvalued species to extinction, so as to devote all of the land resources to production of the more valuable species. Livestock husbandry is this behaviour at the extreme.

In the predator-prey case, the fate of each species is again dependent upon their relative values. Suppose species 1 is a predator ($G_1(x_1, x_2, L) < 0$) and species 2 is its prey ($F_2(x_1, x_2, L) > 0$). Then the interdependence term of Equation (5.5), works against the predator (makes it less valuable), while the corresponding term in Equation (5.6), works in favour of the prey species. If both species have a harvest value, the predator, by reducing the growth of its prey, is reducing the potential returns to the land resource. Conversely, the prey, by increasing the growth of the predator is increasing potential returns. The magnitudes of these impacts are again dependent on the relative value of the two species.

5.1.3 Empirical Results

Once the analytical model has been developed, an empirical model is solved for the three cases of species interaction. Species independence is illustrated using the African Elephant and the White Rhinoceros. The Impala and Greater Kudu illustrate the case of interspecific competition, while the African Lion and the Blue Wildebeest serve as examples of predator-prey interaction.

Turning first to the case of independent species. In the single species result the harvesting of Elephant alone generates an insufficient return to ensure the survival of the species. The model predicts an immediate harvest of Elephants back to 5 percent of initial density (from an initial stock of 9,152 to 540), and thereafter harvesting to keep numbers at this level. The continued presence of Elephants (albeit at critically low levels) probably owes more to the specification of a cost function, making harvesting small populations prohibitively expensive, than to the value derived from the Elephants themselves. This result should therefore be regarded as predicting the extinction of Elephants.

In contrast, the inclusion of the more valuable Rhinoceros (in the multiple species case) affords the Elephant access to the resources necessary for its continued survival, with periodic harvesting approximately every 30 periods. This keeps the

Elephant within a stock limit cycle in the order of half to three and half times initial density (a stock range of 4,500 to 31,200). In effect, the value generated from the continued existence and harvest of the Rhinoceros subsidises continued existence and harvest of the Elephant. This result underlines the potential for misapplication of single species results and illustrates the importance of considering all species of value in management decisions, even in the absence of any direct ecological relationship.

The effect of interspecific competition is clear both in the steady-state stock and harvest levels. The effect of Impala on the Kudu is to reduce the steady-state stock and harvest levels. The greater the level of competition, the further the multiple species outcome falls below the single species result. Similarly, the Impala's multiple species steady-state stock and harvest levels fall below those given by the single species model.

The predator-prey case presents some stark contrasts between the single and multiple species approach. Under a single species model, Lion populations oscillate between 21,000 and 32,000 on a regular six-year cycle. With the inclusion of the Lion's predatory effect on Wildebeest, the multiple species model produces an initial surge in population, followed by a period of rapid decline. This result is of interest in that although a single Lion is of significantly greater value than a single Wildebeest, the size of the Wildebeest population, coupled with the ability of it to grow (and therefore be sustainably harvested) at over twice the rate of the Lion, serves to make the Wildebeest the more attractive option.

Both the single and multiple species models of Wildebeest exhibit similar population dynamics, strong early growth reaching a steady-state stock level. The single species result reaches a long-run steady-state level of approximately 80,000, with annual harvesting of 12,000 animals to maintain populations at this level. The multiple species model initially overshoots the long-run steady-state level of 100,000 with populations reduced to the steady-state level through a combination of heavy harvesting and Lion predation (as Lion populations are strong at this time). The fact that Wildebeest obtain a higher long-run steady-state level when Lions are present is perhaps a result of their value as prey (in addition to their harvestable value).

5.2 Limitations

There are two sources of limitations in a multidisciplinary work such as this: ecological limitations and economic limitations. Each is dealt with separately.

5.2.1 Ecological Limitations

This is by no means an exhaustive review of the ecological limitations of this work. The modelling of population dynamics is fraught with difficulty, and the functional forms used here are subject to a number of limitations, many of which have been discussed previously. The limitations all stem from the same source, an information gap. Without precise functional forms for the growth of the species in question, accurate modelling of population dynamics is problematic. This is further complicated by the necessity, in a multiple species framework, to model not only the growth of the species themselves, but also their interaction with others.

5.2.2 Economic Limitations

There are a number of economic limitations to the approach adopted here, many of which stem from the fact that we are trying to assign value to goods that have, at best, incomplete markets.

In addition to the limitations surrounding the chosen method of calculating harvest values, as discussed in Chapter 4, there is a limitation surrounding the assumption that the only values attributable to species are those derived from their harvest. Clearly this is not the case; species such as the Elephant, Rhinoceros and Lion have significant non-consumptive values and potential to earn income streams from other sources, such as from tourism or donations from conservation groups. Obtaining an estimate of the TEV of wildlife species is an area with considerable scope for further research.

A further limitation is the choice of a fixed value or price of harvest for each species as opposed to the specification of a species demand curve. Current harvest values, in particular trophy fees, are largely based on the relative scarcity of the species in question. Over time, if a species population grows, trophy fees are likely to fall. Conversely, if a species population falls, trophy fees may be expected to rise. As a consequence, the relative values of species, as population levels vary, may converge or may be reversed; that is the high-value species may become low valued and the low-valued species become high value. If this were the case, population dynamics would vary considerably from those presented here. This limitation again suggests further research is needed on the value of species, although the estimation of a demand curve for species such as those considered here would be complex, not only because of an incomplete market and the existence of a black market, but also because policy changes such as a relaxing of the CITES trade ban would have a dramatic effect on prices.

Another limitation is in the estimation of the cost of harvest. Again, this is an issue of incomplete markets; in this case it is the supply curve that is missing. Further research could make it possible to determine a more accurate function for the cost of harvesting terrestrial game species.

An overriding limitation, not simply of the models presented here, but of the bioeconomic modelling of terrestrial species in general, is the assumption that the landowner (or wildlife manager) has the ability to control harvest in such a way as to maximise revenue (and by assumption, welfare). In the case of African game species, incomplete and weakly enforceable property rights reduce the validity of this assumption.

5.3 Conclusions

Although the extent of species loss can be questioned, there is little doubt that human activity is having a profound effect on other species. Economists have been charged with investigating and understanding the incentives behind people's behaviour that lead to the endangerment and possible extinction of species. One of the approaches economists have taken to reach this understanding is to develop bioeconomic models.

To date, these models have been overwhelmingly single species in focus. This thesis questions that approach and explores the implications of introducing multiple species into the single species framework. An outcome of the models developed in Chapters 3 and 4 is that one can infer the conditions under which a single species model may be appropriate, at least in general terms. If species are independent, and either the opportunity cost of capital or the value of habitat is very low relative to the value of the species in question, then a single species model may yield results similar to that of a multiple species model. In this case the burden on species, as given by Equation

(3.30), is negligible while Equations (3.31) and (3.32) become similar to the single species modified golden rule.

Similarly, if the relative value of one species is significantly greater than that of all others in the ecosystem, then a single species model may also approximate the results of a multiple species result. In this case, the interdependence terms are negligible for all except the species of value.

The Rhinoceros, which exhibits similar stock dynamics under both a multiple and single species framework, serves to illustrate the case where a single species model is appropriate. In this model, the Rhinoceros has a sufficiently high value and rate of growth to justify continued allocation of land resource and also has a relative value that makes it indifferent to the introduction of the Elephant.

Of more interest, given the prevalence of single species models in the literature, are the conditions under which a single species model is not appropriate. When species are independent and the value of species is low relative to either the opportunity cost of capital or the value of habitat, a single species model significantly underestimates both optimal stock levels and land allocation. The Elephant best illustrates this case. Under a single species framework, in this model, the value derived from the continued presence and harvest of Elephants is insufficient to justify current land allocation, yet in a multiple species framework, with the inclusion of the more valuable Rhinoceros, current land allocations remain and positive (albeit fluctuating) populations of Elephant exist. Here, the burden on species as given by Equation (3.30) is shouldered by the Rhinoceros, allowing the Elephant 'subsidised' access to land. Without this subsidisation the burden is too great.

This result has important implications for conservation policy. The single species model suggests that the underlying incentive for landowners is to harvest the Elephant to unsustainable levels and convert land to an alternative use. If Elephant conservation is the objective, the policymaker might feel the need to somehow alter these incentives. However, the multiple species model, where the value of the Rhinoceros is considered, suggests that such incentives do not actually exist; that is, land conversion and Elephant extinction are no longer 'optimal'. The misapplication of the single species model could result in policy being designed to address a non-existent problem. While the policy in itself might not harm species directly, conservation funds are limited and any policy that directs resources towards addressing unfounded concerns necessarily diverts funds away from more pressing issues. This leads to sub-optimal conservation outcomes. A significant aspect of this case is that it demonstrates the importance of considering a multiple species framework, even when species appear ecologically independent.

However, species do not live independently; they interact with species with which they share habitat and, when species interact, the potential for misapplication of the single species framework is even greater.

When species compete, the single species framework consistently produces higher stock levels than the multiple species framework; the greater the level of competition, the greater the difference. This is seen in the case of the Impala and the Wildebeest, although significantly positive stocks of each remain under both scenarios.

Where differences are significant or stocks are at a critical level, the potential exists for policy errors to be made as a result of the misapplication of a single species model. Consider the case where a policymaker, witnessing declining stock levels, forms the opinion, using a single species model, of what the steady-state stock level should be. The policymaker therefore, with the expectation that the decline will halt once this level is reached, determines that policy intervention is not warranted. If, however, the steady-state stock level (due to interspecific competition) is in fact significantly lower than the single species model suggests, the policymaker's inaction may inadvertently allow a species to decline to critically low levels, or even extinction.

Conversely, consider the case where the species in question is a pest. If the policymaker forms the opinion, based on a single species model, that steady-state stock levels are likely to be too high, the policymaker might enact a species management programme accordingly. If, however, in the presence of interspecific competition, the steady-state stock level is acceptable, a management programme would be unnecessary and therefore represent an inefficient allocation of limited conservation resources.

Of course, the results discussed above were made on the assumption that the Impala and Wildebeest, as individuals and together, are able to generate sufficient return to justify the continued allocation of habitat (both were modelled with a reduced value of land). In this respect the comments made in regards to interdependent species, namely that including all economically relevant species helps to share the burden of generating this return, also apply in this case.

As discussed in Chapter 3, the relative values of the predator and its prey are critical to determining the outcome of the predator-prey model. When the predator is of greater value there are strong incentives to maintain positive healthy populations of both species: the predator for its harvest value, the prey as a source of food. In this scenario, modelling the predator under a multiple species framework is unlikely to yield significantly different results from the single species case. Again making the assumption that the predator is of sufficient value to justify the continued allocation of habitat, the predator would exhibit similar population dynamics to that of the Rhinoceros in the independent species case. This is evident in the strongly positive stock levels of Lion produced by the single species model. The danger for both the predator and the prey in this case, however, arises from the misapplication of the single species framework to its prey; that is, a single species model only recognises the harvest value of prey, not its contribution to the growth of the predator. Thus, where the prey is of insufficient value to justify the continued allocation of land, it would appear appropriate (under a single species framework) to remove the prey entirely, which of course would have potentially devastating effects for the predator.

When the prey is of greater value, significant potential for misapplication lies in the modelling of the predator. Under a single species framework, it appears as if there is an incentive (given sufficient value to justify continued allocation of land) to maintain positive predator stocks. This is a consequence of the single species model taking into account the value derived from harvesting the predator while ignoring the dampening effect of the predator on prey populations.

For those seeking to conserve predators, the implications of misapplying the single species framework to a predator-prey case are significant. Under a single species framework it appears as if there is an incentive to maintain healthy predator populations, and thus little conservation effort is needed. However, with the inclusion of the dampening effect the predator has on its prey, the multiple species model yields significantly different results. Explicitly, an incentive now exists to remove the predator, thereby allowing the prey to grow unabated; the greater the dampening effect, the greater this incentive.

The implication for policymakers is that to conserve low-valued predator species, incentives must be altered. Without appropriate policy intervention, predators are likely to be harvested to critical levels, a result in direct contrast to the policy recommendations that would be formed under a single species framework.

The current plight of many predators, including the African Lion and the African Wild Dog, is consistent with the multiple species models results. Both of these species have experienced significant population decline, primarily due to the actions of landowners seeking to protect their stock. The predator-prey model, in particular the case where the predator is of little value, strongly supports the thesis that misapplying single species models to multiple species situations could result in deceptive results and incorrect policy decisions.

In all, the conditions under which a single species model is sufficient, namely when species are independent and the opportunity cost of capital or the cost of land is low, or the species in question is of far greater economic significance than all others, are clearly restrictive. If these conditions are not met, a single species framework will produce unreliable results. In certain cases of species interaction, such as where competition between species is slight or where a predator is of greater value than its prey, and again the opportunity cost of capital or the cost of land is low, these inaccuracies may be insignificant. For most species in most habitats a single species model is insufficient.

However, the cost and complexity of developing multiple species models often preclude their use in some situations. If a single species approach is necessary, it is important to recognise the limitations of this approach. In particular, it is useful to understand the likely direction of any errors. For species of insufficient value to justify land allocation on their own, irrespective of the ecological relationship they have with the species with which they share their habitat, a single species model is likely to severely underestimate optimal populations. When species are in competition, single species models are likely to overestimate optimal stocks, with the overestimation increasing as the level of competition increases. For predator-prey the situation is not as clear. In the case where the predator is of greater value, a single species model of prey is likely to underestimate its optimal stock level. When the prey is of greater value, a single species model is likely to vastly exaggerate optimal predator populations.

This thesis demonstrates that the inclusion of at least all economically valuable species in an ecosystem is important when constructing bioeconomic models. Using single species models where multiple species are economically significant could lead to misleading results and ultimately to incorrect policy decisions.

APPENDICES

APPENDIX A - GAMS COMMAND FILE FOR AFRICAN ELEPHANT – SINGLE SPECIES

```
*Elephant Model - Single Species Model
*turns off extra output
*settings and limits equation output
$offsymxref offsymlist
options limrow=0, limcol=0, solprint=off, decimals=4, iterlim=10000;
*sets time periods in this case 150
 set t time periods /0*150/;
*sets the discount factor (in this case based upon a discount rate of 5 percent)
 parameter df(t) disc factor;
df(t) = (1.0/(1.0+0.05))**(ord(t)-1)
*defines scalars Note these have been divided by 1000 (excluding discount rate)
scalar xo initial stock /9.152/;
scalar co initial cost of harvest /6.5/;
scalar r intrinsic growth rate /0.065/;
scalar k carrying capacity /100.00/;
scalar p price of harvest /14.5/;
scalar d discount rate /0.05/;
scalar pl price of land /300000/;
*defines state and control variables
positive variables
x(t) stock at time t
h(t) harvest at time t
l(t) allocation of land at time t;
free variable
dnr discounted net revenue;
*equations
equations NSW definition of net social welfare
          growth(t) change in stock
          lancon(t) land constraint
          lanconl(t) land constraint
          harvcon(t) harvest constraint;
NSW.. DNR =e= sum(t,df(t)*(p*h(t)-(co*xo/x(t))*h(t)-d*pl*L(t)));
growth(t+1).. x(t+1) =e= x(t)+r*x(t)*(1-(x(t)/(k*L(t))))-H(t);
lancon(t).. x(t) =l= k*l(t);
lanconl(t).. l(t) =l= 1;
harvcon(t).. x(t) =g= h(t);
*define bounds, starting values, and intial conditions x.lo(t) .001;
x.up(t)     = 300;
x.lo(t) = .001;
l.lo(t)      = 0.001;
l.up(t) = 10;
*starting value
 x.l(t) = 9.152;
 h.l(t) = .1;
l.l(t) = 1;
*initial condiiton (time period 0)
x.fx("0") = xo;
l.fx("0") = 1;
h.lo(t) = 0.0001;
h.up(t) = 200;
*solve the model using nlp
model ssc/all/;
option nlp=conopt2;
solve ssc using nlp maximising dnr;
parameter opt optimal values of given variables;
opt(t,"xstar") = x.l(t)*1000;
opt(t,"hstar") = h.l(t)*1000;
opt(t,"lstar") = l.l(t);
display opt;
```

APPENDIX B - GAMS COMMAND FILE FOR WHITE RHINOCEROS – SINGLE SPECIES

```
*Rhinoceros Model - Single Species Model
*turns off extra output
*settings and limits equation output
$offsymxref offsymlist
options limrow=0, limcol=0, solprint=off, decimals=4, iterlim=10000;
*sets time periods in this case 150
 set t time periods /0*150/;
*sets the discount factor (in this case based upon a discount rate of 5 percent)
 parameter df(t) disc factor;
df(t) = (1.0/(1.0+0.05))**(ord(t)-1)
*defines scalars Note these have been divided by 1000 (excluding discount rate)
scalar xo initial stock /2.5/;
scalar co initial cost of harvest /7.5/;
scalar r intrinsic growth rate /0.09/;
scalar k carrying capacity /100.00/;
scalar p price of harvest /37.5/;
scalar d discount rate /0.05/;
scalar pl price of land /300000/;
*defines state and control variables
positive variables
x(t) stock at time t
h(t) harvest at time t
l(t) allocation of land at time t;
free variable
dnr discounted net revenue;
*equations
equations NSW definition of net social welfare
          growth(t) change in stock
          lancon(t) land constraint
          lanconl(t) land constraint
          harvcon(t) harvest constraint;
NSW.. DNR =e= sum(t,df(t)*(p*h(t)-(co*xo/x(t))*h(t)-d*pl*L(t)));
growth(t+1).. x(t+1) =e= x(t)+r*x(t)*(1-(x(t)/(k*L(t))))-H(t);
lancon(t).. x(t) =l= k*l(t);
lanconl(t).. l(t) =l= 1;
harvcon(t).. x(t) =g= h(t);
*define bounds, starting values, and intial conditions x.lo(t) .001;
x.up(t)    = 300;
x.lo(t) = .001;
l.lo(t)    = 0.001;
l.up(t) = 10;
*starting value
 x.l(t) = 2.5;
 h.l(t) = .1;
l.l(t) = 1;
*initial condiiton (time period 0)
x.fx("0") = xo;
l.fx("0") = 1;
h.lo(t) = 0.0001;
h.up(t) = 200;
*solve the model using nlp
model ssc/all/;
option nlp=conopt2;
solve ssc using nlp maximising dnr;
parameter opt optimal values of given variables;
opt(t,"xstar") = x.l(t)*1000;
opt(t,"hstar") = h.l(t)*1000;
opt(t,"lstar") = l.l(t);
display opt;
```

APPENDIX C - GAMS COMMAND FILE FOR AFRICAN ELEPHANT AND WHITE RHINOCEROS – INDEPENDENT SPECIES

```
*Independent Multiple Species Model
*turns off extra output
*settings and limits equation output
$offsymxref offsymlist
options limrow=0, limcol=0, solprint=off, decimals=4, iterlim=10000;
*sets time periods in this case 150
 set t time periods /0*150/;
*sets the discount factor (in this case based upon a discount rate of 5 percent)
 parameter df(t) disc factor;
df(t) = (1.0/(1.0+0.05))**(ord(t)-1)
*defines scalars Note these have been divided by 1000 (excluding discount rate)
scalar xo1 initial stock species 1 /9.152/;
scalar xo2 initial stock species 2 /2.5/;
scalar co1 initial cost of harvest species 1 /6.5/;
scalar co2 initial cost of harvest species 2 /7.5/;
scalar r1 intrinsic growth rate of species 1 /0.065/;
scalar r2 intrinsic growth rate of species 2 /0.09/;
scalar k1 carrying capacity of species 1 /100.00/;
scalar k2 carrying capacity of species 2 /100.00/;
scalar p1 price of harvest of species 1 /14.5/;
scalar p2 price of harvest of species 2 /37.5/;
scalar d discount rate /0.05/;
scalar pl price of land /300000/;
*defines state and control variables
positive variables
x1(t) stock of species 1 at time t
x2(t) stock of species 2 at time t
h1(t) harvest of species 1 at time t
h2(t) harvest at species 2 at time t
l(t) allocation of land at time t;
free variable
dnr discounted net revenue;
*equations
equations NSW definition of net social welfare
          growth1(t) change in stock of species 1
          growth2(t) change in stock of species 2
          lancon1(t) land constraint species 1
          lancon2(t) land constraint species 2
          lanconl(t) land constraint
          harvcon1(t) harvest constraint species 1
          harvcon2(t) harvest constraint species 2;
NSW.. DNR =e= sum(t,df(t)*(p1*h1(t)-(co1*xo1/x1(t))*h1(t))+((p2*h2(t)-(co2*xo2/x2(t)))-d*pl*L(t)));
growth1(t+1).. x1(t+1) =e= x1(t)+r1*x1(t)*(1-x1(t)/(k1*L(t)))-h1(t);
growth2(t+1).. x2(t+1) =e= x2(t)+r2*x2(t)*(1-x2(t)/(k2*L(t)))-h2(t);
lancon1(t).. x1(t) =l= k1*l(t);
lancon2(t).. x2(t) =l= k2*l(t);
lanconl(t).. l(t) =l= 1;
harvcon1(t).. x1(t) =g= h1(t);
harvcon2(t).. x2(t) =g= h2(t);
*define bounds, starting values, and intial conditions x.lo(t) .001;
x1.lo(t) = .001;
x2.lo(t) = .001;
x1.up(t) = 300;
x2.up(t) = 300;
l.lo(t)    = 0.001;
l.up(t) = 10;
*starting value
x1.l(t) = 9.152;
x2.l(t) = 2.5;
h1.l(t) = .1;
h2 l(t) = .1;
```

```
l.l(t) = 1;
*initial condiiton (time period 0)
x1.fx("0") = xo1;
x2.fx("0") = xo2;
l.fx("0") = 1;
h1.lo(t) = 0.0001;
h2.lo(t) = 0.0001;
h1.up(t) = 200;
h2.up(t) = 200;
*solve the model using nlp
model ssc/all/;
option nlp=conopt2;
solve ssc using nlp maximising dnr;
parameter opt optimal values of given variables;
opt(t,"x1star") = x1.l(t)*1000;
opt(t,"h1star") = h1.l(t)*1000;
opt(t,"x2star") = x2.l(t)*1000;
opt(t,"h2star") = h2.l(t)*1000;
opt(t,"lstar") = l.l(t);
display opt;
```

APPENDIX D - GAMS COMMAND FILE FOR IMPALA – SINGLE SPECIES

```
*Impala Model - Single Species Model
*turns off extra output
*settings and limits equation output
$offsymxref offsymlist
options limrow=0, limcol=0, solprint=off, decimals=4, iterlim=10000;
*sets time periods in this case 150
 set t time periods /0*150/;
*sets the discount factor (in this case based upon a discount rate of 5 percent)
 parameter df(t) disc factor;
df(t) = (1.0/(1.0+0.05))**(ord(t)-1)
*defines scalars Note these have been divided by 1000 (excluding discount rate)
scalar xo initial stock /100/;
scalar co initial cost of harvest /0.35/;
scalar r intrinsic growth rate /0.35/;
scalar k carrying capacity /400.00/;
scalar p price of harvest /0.6/;
scalar d discount rate /0.05/;
scalar pl price of land /30000/;
*defines state and control variables
positive variables
x(t) stock at time t
h(t) harvest at time t
l(t) allocation of land at time t;
free variable
dnr discounted net revenue;
*equations
equations NSW definition of net social welfare
          growth(t) change in stock
          lancon(t) land constraint
          lanconl(t) land constraint
          harvcon(t) harvest constraint;
NSW.. DNR =e= sum(t,df(t)*(p*h(t)-(co*xo/x(t))*h(t)-d*pl*L(t)));
growth(t+1).. x(t+1) =e= x(t)+r*x(t)*(1-(x(t)/(k*L(t))))-H(t);
lancon(t).. x(t) =l= k*l(t);
lanconl(t).. l(t) =l= 1;
harvcon(t).. x(t) =g= h(t);
*define bounds, starting values, and intial conditions x.lo(t) .001;
x.up(t)   = 300;
x.lo(t) = .001;
l.lo(t)    = 0.001;
l.up(t) = 10;
*starting value
 x.l(t) = 9.152;
 h.l(t) = .1;
l.l(t) = 1;
*initial condiiton (time period 0)
x.fx("0") = xo;
l.fx("0") = 1;
h.lo(t) = 0.0001;
h.up(t) = 200;
*solve the model using nlp
model ssc/all/;
option nlp=conopt2;
solve ssc using nlp maximising dnr;
parameter opt optimal values of given variables;
opt(t,"xstar") = x.l(t)*1000;
opt(t,"hstar") = h.l(t)*1000;
opt(t,"lstar") = l.l(t);
display opt;
```

APPENDIX E - GAMS COMMAND FILE FOR GREATER KUDU – SINGLE SPECIES

```
*Kudu Model - Single Species Model
*turns off extra output
*settings and limits equation output
$offsymxref offsymlist
options limrow=0, limcol=0, solprint=off, decimals=4, iterlim=10000;
*sets time periods in this case 150
 set t time periods /0*150/;
*sets the discount factor (in this case based upon a discount rate of 5 percent)
 parameter df(t) disc factor;
df(t) = (1.0/(1.0+0.05))**(ord(t)-1)
*defines scalars Note these have been divided by 1000 (excluding discount rate)
scalar xo initial stock /3.5/;
scalar co initial cost of harvest /0.35/;
scalar r intrinsic growth rate /0.20/;
scalar k carrying capacity /300.00/;
scalar p price of harvest /1.35/;
scalar d discount rate /0.05/;
scalar pl price of land /30000/;
*defines state and control variables
positive variables
x(t) stock at time t
h(t) harvest at time t
l(t) allocation of land at time t;
free variable
dnr discounted net revenue;
*equations
equations NSW definition of net social welfare
          growth(t) change in stock
          lancon(t) land constraint
          lanconl(t) land constraint
          harvcon(t) harvest constraint;
NSW.. DNR =e= sum(t,df(t)*(p*h(t)-(co*xo/x(t))*h(t)-d*pl*L(t)));
growth(t+1).. x(t+1) =e= x(t)+r*x(t)*(1-(x(t)/(k*L(t))))-H(t);
lancon(t).. x(t) =l= k*l(t);
lanconl(t).. l(t) =l= 1;
harvcon(t).. x(t) =g= h(t);
*define bounds, starting values, and intial conditions x.lo(t) .001;
x.up(t)    = 300;
x.lo(t) = .001;
l.lo(t)     = 0.001;
l.up(t) = 10;
*starting value
 x.l(t) = 9.152;
 h.l(t) = .1;
l.l(t) = 1;
*initial condiiton (time period 0)
x.fx("0") = xo;
l.fx("0") = 1;
h.lo(t) = 0.0001;
h.up(t) = 200;
*solve the model using nlp
model ssc/all/;
option nlp=conopt2;
solve ssc using nlp maximising dnr;
parameter opt optimal values of given variables;
opt(t,"xstar") = x.l(t)*1000;
opt(t,"hstar") = h.l(t)*1000;
opt(t,"lstar") = l.l(t);
display opt;
```

APPENDIX F - GAMS COMMAND FILE FOR IMPALA AND GREATER KUDU – INTERSPECIFIC COMPETITION

```
*Interspecific Competition Multiple Species Model - Mid
*turns off extra output
*settings and limits equation output
$offsymxref offsymlist
options limrow=0, limcol=0, solprint=off, decimals=4, iterlim=10000;
*sets time periods in this case 150
 set t time periods /0*150/;
*sets the discount factor (in this case based upon a discount rate of 5 percent)
 parameter df(t) disc factor;
df(t) = (1.0/(1.0+0.05))**(ord(t)-1)
*defines scalars Note these have been divided by 1000 (excluding discount rate)
scalar xo1 initial stock species 1 /100/;
scalar xo2 initial stock species 2 /3.5/;
scalar co1 initial cost of harvest species 1 /0.35/;
scalar co2 initial cost of harvest species 2 /0.35/;
scalar r1 intrinsic growth rate of species 1 /0.35/;
scalar r2 intrinsic growth rate of species 2 /0.20/;
scalar k1 carrying capacity of species 1 /400.00/;
scalar k2 carrying capacity of species 2 /300.00/;
scalar p1 price of harvest of species 1 /0.6/;
scalar p2 price of harvest of species 2 /1.35/;
scalar a1 alpha1 effect of species 2 on growth of species 1 /0.665/;
scalar a2 alpha2 effect of species 1 on growth of species 2 /0.375/;
scalar d discount rate /0.05/;
scalar pl price of land /30000/;
*defines state and control variables
positive variables
x1(t) stock of species 1 at time t
x2(t) stock of species 2 at time t
h1(t) harvest of species 1 at time t
h2(t) harvest at species 2 at time t
l(t) allocation of land at time t;
free variable
dnr discounted net revenue;
*equations
equations NSW definition of net social welfare
          growth1(t) change in stock of species 1
          growth2(t) change in stock of species 2
          lancon1(t) land constraint species 1
          lancon2(t) land constraint species 2
          lanconl(t) land constraint
          harvcon1(t) harvest constraint species 1
          harvcon2(t) harvest constraint species 2;
NSW.. DNR =e= sum(t,df(t)*(p1*h1(t)-(co1*xo1/x1(t))*h1(t))+((p2*h2(t)-(co2*xo2/x2(t)))-d*pl*L(t)));
growth1(t+1).. x1(t+1) =e= x1(t)+r1*x1(t)*(1-((x1(t)/(k1*L(t)))+(a1*x2(t)/k1*l(t))))-h1(t);
growth2(t+1).. x2(t+1) =e= x2(t)+r2*x2(t)*(1-((x2(t)/(k2*L(t)))+(a2*x1(t)/k2*l(t))))-h2(t);
lancon1(t).. x1(t) =l= k1*l(t);
lancon2(t).. x2(t) =l= k2*l(t);
lanconl(t).. l(t) =l= 1;
harvcon1(t).. x1(t) =g= h1(t);
harvcon2(t).. x2(t) =g= h2(t);
*define bounds, starting values, and intial conditions x.lo(t) .001;
x1.lo(t) = .001;
x2.lo(t) = .001;
x1.up(t) = 500;
x2.up(t) = 500;
l.lo(t)      = 0.001;
l.up(t) = 10;
*starting value
x1.l(t) = 9.152;
x2.l(t) = 2.5,
h1.l(t) = .1;
```

```
h2.l(t) = .1;
l.l(t) = 1;
*initial condiiton (time period 0)
x1.fx("0") = xo1;
x2.fx("0") = xo2;
l.fx("0") = 1;
h1.lo(t) = 0.0001;
h2.lo(t) = 0.0001;
h1.up(t) = 200;
h2.up(t) = 200;
*solve the model using nlp
model ssc/all/;
option nlp=conopt2;
solve ssc using nlp maximising dnr;
parameter opt optimal values of given variables;
opt(t,"x1star") = x1.l(t)*1000;
opt(t,"h1star") = h1.l(t)*1000;
opt(t,"x2star") = x2.l(t)*1000;
opt(t,"h2star") = h2.l(t)*1000;
opt(t,"lstar") = l.l(t);
display opt;
```

APPENDIX G - GAMS COMMAND FILE FOR AFRICAN LION – SINGLE SPECIES

```
*Lion Model - Single Species Model
*turns off extra output
*settings and limits equation output
$offsymxref offsymlist
options limrow=0, limcol=0, solprint=off, decimals=4, iterlim=10000;
*sets time periods in this case 150
 set t time periods /0*150/;
*sets the discount factor (in this case based upon a discount rate of 5 percent)
 parameter df(t) disc factor;
df(t) = (1.0/(1.0+0.05))**(ord(t)-1)
*defines scalars Note these have been divided by 1000 (excluding discount rate)
scalar xo initial stock /2.5/;
scalar co initial cost of harvest /6.5/;
scalar r intrinsic growth rate /0.11/;
scalar k carrying capacity /100.00/;
scalar p price of harvest /13.5/;
scalar d discount rate /0.05/;
scalar pl price of land /30000/;
*defines state and control variables
positive variables
x(t) stock at time t
h(t) harvest at time t
l(t) allocation of land at time t;
free variable
dnr discounted net revenue;
*equations
equations NSW definition of net social welfare
          growth(t) change in stock
          lancon(t) land constraint
          lanconl(t) land constraint
          harvcon(t) harvest constraint;
NSW.. DNR =e= sum(t,df(t)*(p*h(t)-(co*xo/x(t))*h(t)-d*pl*L(t)));
growth(t+1).. x(t+1) =e= x(t)+r*x(t)*(1-(x(t)/(k*L(t))))-H(t);
lancon(t).. x(t) =l= k*l(t);
lanconl(t).. l(t) =l= 1;
harvcon(t).. x(t) =g= h(t);
*define bounds, starting values, and intial conditions x.lo(t) .001;
x.up(t)   = 300;
x.lo(t) = .001;
l.lo(t)    = 0.001;
l.up(t) = 10;
*starting value
 x.l(t) = 9.152;
 h.l(t) = .1;
l.l(t) = 1;
*initial condiiton (time period 0)
x.fx("0") = xo;
l.fx("0") = 1;
h.lo(t) = 0.0001;
h.up(t) = 200;
*solve the model using nlp
model ssc/all/;
option nlp=conopt2;
solve ssc using nlp maximising dnr;
parameter opt optimal values of given variables;
opt(t,"xstar") = x.l(t)*1000;
opt(t,"hstar") = h.l(t)*1000;
opt(t,"lstar") = l.l(t);
display opt;
```

APPENDIX H - GAMS COMMAND FILE FOR BLUE WILDEBEEST – SINGLE SPECIES

```
*Wildebeest Model - Single Species Model
*turns off extra output
*settings and limits equation output
$offsymxref offsymlist
options limrow=0, limcol=0, solprint=off, decimals=4, iterlim=10000;
*sets time periods in this case 150
 set t time periods /0*150/;
*sets the discount factor (in this case based upon a discount rate of 5 percent)
 parameter df(t) disc factor;
df(t) = (1.0/(1.0+0.05))**(ord(t)-1)
*defines scalars Note these have been divided by 1000 (excluding discount rate)
scalar xo initial stock /14/;
scalar co initial cost of harvest /0.35/;
scalar r intrinsic growth rate /0.25/;
scalar k carrying capacity /200.00/;
scalar p price of harvest /1.15/;
scalar d discount rate /0.05/;
scalar pl price of land /30000/;
*defines state and control variables
positive variables
x(t) stock at time t
h(t) harvest at time t
l(t) allocation of land at time t;
free variable
dnr discounted net revenue;
*equations
equations NSW definition of net social welfare
            growth(t) change in stock
            lancon(t) land constraint
            lanconl(t) land constraint
            harvcon(t) harvest constraint;
NSW.. DNR =e= sum(t,df(t)*(p*h(t)-(co*xo/x(t))*h(t)-d*pl*L(t)));
growth(t+1).. x(t+1) =e= x(t)+r*x(t)*(1-(x(t)/(k*L(t))))-H(t);
lancon(t).. x(t) =l= k*l(t);
lanconl(t).. l(t) =l= 1;
harvcon(t).. x(t) =g= h(t);
*define bounds, starting values, and intial conditions x.lo(t) .001;
x.up(t)    = 300;
x.lo(t) = .001;
l.lo(t)     = 0.001;
l.up(t) = 10;
*starting value
 x.l(t) = 9.152;
 h.l(t) = .1;
l.l(t) = 1;
*initial condiiton (time period 0)
x.fx("0") = xo;
l.fx("0") = 1;
h.lo(t) = 0.0001;
h.up(t) = 200;
*solve the model using nlp
model ssc/all/;
option nlp=conopt2;
solve ssc using nlp maximising dnr;
parameter opt optimal values of given variables;
opt(t,"xstar") = x.l(t)*1000;
opt(t,"hstar") = h.l(t)*1000;
opt(t,"lstar") = l.l(t);
display opt;
```

APPENDIX I - GAMS COMMAND FILE FOR AFRICAN LION AND BLUE WILDEBEEST – PREDATOR-PREY

```
*Predator-Prey Multiple Species Model- mid
*turns off extra output
*settings and limits equation output
$offsymxref offsymlist
options limrow=0, limcol=0, solprint=off, decimals=4, iterlim=10000;
*sets time periods in this case 150
 set t time periods /0*150/;
*sets the discount factor (in this case based upon a discount rate of 5 percent)
 parameter df(t) disc factor;
df(t) = (1.0/(1.0+0.05))**(ord(t)-1)
*defines scalars Note these have been divided by 1000 (excluding discount rate)
scalar xo1 initial stock species 1 /2.5/;
scalar xo2 initial stock species 2 /14/;
scalar co1 initial cost of harvest species 1 /6.5/;
scalar co2 initial cost of harvest species 2 /0.35/;
scalar r1 intrinsic growth rate of species 1 /0.11/;
scalar r2 intrinsic growth rate of species 2 /0.25/;
scalar k1 carrying capacity of species 1 /100.00/;
scalar k2 carrying capacity of species 2 /200.00/;
scalar p1 price of harvest of species 1 /13.5/;
scalar p2 price of harvest of species 2 /1.15/;
scalar a1 alpha1 effect of species 2 on growth of species 1 /0.25/;
scalar a2 alpha2 effect of species 1 on growth of species 2 /1.00/;
scalar d discount rate /0.05/;
scalar pl price of land /30000/;
*defines state and control variables
positive variables
x1(t) stock of species 1 at time t
x2(t) stock of species 2 at time t
h1(t) harvest of species 1 at time t
h2(t) harvest at species 2 at time t
l(t) allocation of land at time t;
free variable
dnr discounted net revenue;
*equations
equations NSW definition of net social welfare
          growth1(t) change in stock of species 1
          growth2(t) change in stock of species 2
          lancon1(t) land constraint species 1
          lancon2(t) land constraint species 2
          lanconl(t) land constraint
          harvcon1(t) harvest constraint species 1
          harvcon2(t) harvest constraint species 2;
NSW.. DNR =e= sum(t,df(t)*(p1*h1(t)-(co1*xo1/x1(t))*h1(t))+((p2*h2(t)-(co2*xo2/x2(t)))-d*pl*L(t)));
growth1(t+1).. x1(t+1) =e= x1(t)+r1*x1(t)*(1-((x1(t)/(k1*L(t)))-(a1*x2(t)/k1*l(t))))-h1(t);
growth2(t+1).. x2(t+1) =e= x2(t)+r2*x2(t)*(1-((x2(t)/(k2*L(t)))+(a2*x1(t)/k2*l(t))))-h2(t);
lancon1(t).. x1(t) =l= k1*l(t);
lancon2(t).. x2(t) =l= k2*l(t);
lanconl(t).. l(t) =l= 1;
harvcon1(t).. x1(t) =g= h1(t);
harvcon2(t).. x2(t) =g= h2(t);
*define bounds, starting values, and intial conditions x.lo(t) .001;
x1.lo(t) = .001;
x2.lo(t) = .001;
x1.up(t) = 500;
x2.up(t) = 500;
l.lo(t)     = 0.001;
l.up(t) = 10;
*starting value
x1.l(t) = 9.152;
x2.l(t) = 2.5;
h1.l(t) = .1;
h2.l(t) = .1;
l.l(t) = 1;
```

```
*initial condiiton (time period 0)
x1.fx("0") = xo1;
x2.fx("0") = xo2;
l.fx("0") = 1;
h1.lo(t) = 0.0001;
h2.lo(t) = 0.0001;
h1.up(t) = 200;
h2.up(t) = 200;
*solve the model using nlp
model ssc/all/;
option nlp=conopt2;
solve ssc using nlp maximising dnr;
parameter opt optimal values of given variables;
opt(t,"x1star") = x1.l(t)*1000;
opt(t,"h1star") = h1.l(t)*1000;
opt(t,"x2star") = x2.l(t)*1000;
opt(t,"h2star") = h2.l(t)*1000;
opt(t,"lstar") = l.l(t);
display opt;
```

REFERENCES

African Lion Working Group. (2000). (Online) Available: http://www.african-lion.org/lions_e.htm (2001,October 12).

African Safari Consultants. (2002). (Online) Available: http://www.safariconsultants.com/hgsa.htm (2001, August 22).

Alexander, R. (2000). "Modelling Species Extinction: The Case for Non-consumptive Values." *Ecological Economics,* 35, 259-269.

Alexander, R. and Shields, D. (2002). "Using Land as a Control Variable in Density-dependent Bioeconomic Models." *Discussion Paper in Natural Resource and Environmental Economics*, No. 22, Centre for Applied Economics and Policy, Massey University, New Zealand.

Alroy, J. (2001). "A Multispecies Overkill Simulation of the End-Pleistocene Megafaunal Mass Extinction." *Science,* 292, 1893-1896.

Bachmura, F. (1971). "The Economics of Vanishing Species." *Natural Resources Journal,* 11(4), 674-692.

Barbier, E., Burgess, J. and Folke, C. (1994). *Paradise Lost? The Ecological Economics of Biodiversity.* London: Earthscan.

Barnes, R., Craig, G., Dublin, H., Overton, G., Simons, W. and Thouless, C. (1999). "African Elephant Database 1998." *Occasional Paper of the IUCN Species Survival Commission*, No. 22, IUCN, Switzerland.

Barnett, H. and Morse, C. (1963). *Scarcity and Growth: The Economics of Natural Resource Availability*. Baltimore: The John Hopkins Press.

Baumgartner, S. (2000). *Ambivalent Joint Production and the Natural Environment: An Economic and Thermodynamic Analysis*. New York: Physica-Verlag.

Baumgartner, S., Dyckhoff, H., Faber, M., Proops, J. and Schiller, J. (2001). "The Concept of Joint Production and Ecological Economics." *Ecological Economics,* 36, 365-372.

Beattie, B. and Taylor, C. (1985). *The Economics of Production.* New York: John Wiley & Sons.

Beckerman, W. (1974). *In Defence of Economic Growth.* London: Johnathon Cape.

Beddington, J., Watts, C. and Wright, W. (1975). "Optimal Cropping of Self-Reproducible Natural Resources." *Econometrica,* 43, 789-802.

Begon, M., Harper, J. and Townsend, C. (1996). *Ecology (3rd ed.).* Oxford: Blackwell Science.

Bell, R. (1987). "Conservation with a Human Face: Conflict and Reconciliation on African Land Use Planning." In Martin, R. (2000). "CITES and the CBD." In Hutton, J. and Dickson, B. (Eds.). (2000). *Endangered Species Threatened Convention: The Past, Present and Future of CITES.* London: Earthscan.

Bentham, J. (1789). *An Introduction to the Principles of Morals and Legislation.* Reprinted: 1948. New York: L.J. LaFleur.

Berck, P. (1979). "Open Access and Extinction." *Econometrica,* 47(4), 877-882.

Blaug, M. (1997). *Economic Theory in Retrospect (5th ed.).* Cambridge, UK: Cambridge University Press.

Boucher, D., James, S. and Keeler, K. (1982). "The Ecology of Mutualism." *Annual Review of Ecological Systems,* 13, 315-347.

Boulding, K. (1966). "The Economics of the Coming Spaceship Earth." In Jarrett, H. (Ed.). *Environmental Quality in a Growing Economy* (pp.3-14). Baltimore: Resources for the Future/John Hopkins University Press.

Brooke, A., Kendrick, D. and Murows, A. (1992). *GAMS Release 2.25: A User's Guide.* New York: Scientific Press.

Brown, L. (1992). *State of the World 1992: A Worldwatch Institute Report on Progress Toward a Sustainable Society.* New York: W.W. Norton & Co.

Bucher, E. (1992). "The Causes and Consequences of Extinction of the Passenger Pigeon." *Current Ornithology,* 9, 1-36.

Bulte, E. and van Kooten, G. (1996). "A Note on Ivory Trade and Elephant Conservation." *Environment and Development Economics,* 1(4), 433-443.

Bulte, E. and van Kooten, G. (1999). "Economic Efficiency, Resource Conservation and the Ivory Trade Ban." *Ecological Economics,* 28, 171-181.

Bulte, E. and van Kooten, G. (1999a). "Economics of Antipoaching Enforcement and the Ivory Trade Ban." *American Journal of Agricultural Economics,* 81, 453-466.

Bulte, E. and van Kooten, G. (1999b). "Metapopulation Dynamics and Stochastic Bioeconomic Modelling." *Ecological Economics,* 30, 293-299.

Bulte, E. and van Kooten, G. (2001). "Harvesting and Conserving a Species When Numbers are Low: Population Viability and Gamblers Ruin in Bioeconomic Models." *Ecological Economics,* 37, 87-100.

Ciriacy-Wantrup, S. (1952). *Resource Conservation: Economics and Politics.* California: University of California Press.

Clark, C. (1973). "Profit Maximisation and the Extinction of Animal Species." *Journal of Political Economy*, 81, 950-961.

Clark, C. (1976). *Mathematical Bioeconomics: The Optimal Management of Renewable Resources*. New York: John Wiley & Sons.

Clark, C. (1990). *Bioeconomic Modelling and Fisheries Management.* New York: John Wiley & Sons.

Clark, C., Clarke, F. and Munro, G. (1979). "The Optimal Exploitation of Renewable Resource Stocks: Problems of Irreversible Investment." *Econometrica,* 47, 25-47.

Coase, R. (1960). "The Problem of Social Cost." *Journal of Law and Economics*, 142-171. Reprinted in Dorfman, R and Dorfman, N. (Eds.). (1977). *Economics of the Environment (2^{nd} ed.)*. Canada: W.W Norton & Co.

Coates, S. (2002, April 9). "Fears of New Ivory Trade." *The Dominion*, p. 4.

Connell, J. (1983). "On the Prevalence and Relative Importance of Interspecific Competition: Evidence from Field Experiments." *The American Naturalist,* 122(5), 661-696.

Connell, J., Mertz, D. and Murdoch, W. (Eds.). (1970). *Readings in Ecology and Ecological Genetics.* New York: Harper Row.

Conrad, J. and Clark, C. (1987). *Natural Resource Economics: Notes and Problems.* Cambridge, UK: Cambridge University Press.

Costanza, J., Perrings, C. and Cleveland, C. (Eds.). (1997). *The Development of Ecological Economics.* Cheltenham, UK: Edward Elgar Publishing Company.

Courtney, L. (1897). "Jevons' Coal Question: Thirty Years After." *Journal of the Royal Statistical Society,* 15(4), 789-810. In Fisher, A. and Peterson, F. (1977). "The Exploitation of Extractive Resources: A Survey." *The Economic Journal,* 87, 681-721.

Cuvier, G. (1799). "Memoir Sur Les Especes D'elephants Vivantes Et Fossiles." *Memoires De L'Academie Des Sciences de Paris*, 2, 1-32. In Hoffman, A. (1989) "Changing Palaeontolgical Views on Mass Extinction Phenomena." In Donovan, S. (Ed.). (1989). *Mass Extinctions: Processes and Evidence* (pp. 1-18). London: Belhaven Press.

Daly, H. (1968). "On Economics As a Life Science." *Journal of Political Economy,* 76, 392-406.

Daly, H. (1992). "Allocation, Distribution and Scale: Towards an Economics that is Efficient, Just and Sustainable." *Ecological Economics,* 6, 185-193.

du Plessis, M. (2000). "CITES and the Causes of Extinction." In Hutton, J. and Dickson, B. (Eds.). (2000). *Endangered Species Threatened Convention: The Past, Present and Future of CITES* (pp. 13-25). London: Earthscan.

ECOAFRICA (2002). "Kruger National Park Flora and Fauna and Climate." (Online) Available: http://www.ecoafrica.com/SAPARKS/IDXKRUG.HTM (2002, January 10).

Edwards-Jones, G., Davies, B. and Hussain, S. (2000). *Ecological Economics.* Oxford UK: Blackwell Science.

Ehrlich, P. (1986). "Extinction: What is Happening Now and What Needs to be Done." In Elliot, D. (Ed.). (1986). *Dynamics of Extinction* (pp.157-164). New York: John Wiley & Sons.

Eldredge, N. (1998). "Life in the Balance." *Natural History,* 107(5), *42-53.*

Emslie, R. and Brooks, M. (Eds.). (1999). *Status Survey and Conservation Action Plan: African Rhino*. London: IUCN.

Fairall, N. (1982). "Production Parameters of the Impala, *Aepyceros melampus*." *South African Journal of Animal Science,* 13(3), 176-179.

Falkena, H. (2000). *Bulls, Bears and Lions: Game Ranch Profitability in Southern Africa.* Durbin: SA Financial Sector Forum.

Fisher, A. and Peterson, F. (1976). "The Environment in Economics: A Survey." *Journal of Economic Literature*, 14, 1-33.

Fisher, A. and Peterson, F. (1977). "The Exploitation of Extractive Resources: A Survey." *The Economic Journal,* 87, 681-721.

GAMS. (1998). "GamsEdit Information." (Online) Available: http://www.eco.rug.nl/medewerk/thissen/ (2001, July 2).

Garland, R. (1989). "Terrestrial Environmental Changes and Extinction Patterns at the Cretaceous-Tertiary Boundary, North America." In Donovan, S. (Ed.). (1989). *Mass Extinctions: Processes and Evidence* (pp. 195-216). London: Belhaven Press.

Gause, G. (1932). "Experimental Studies on the Struggle for Existence: Mixed Population of Two Species of Yeast." *Journal of Experimental Biology,* 9, 389-402.

Gause, G. (1934). *The Struggle for Existence.* New York: Hafner

Georgescu-Roegen, N. (1971). *The Entropy Law and the Economic Process.* Cambridge, MA: Harvard University Press.

Gordon, H. (1954). "The Economic Theory of a Common-Property Resource: The Fishery." *The Journal of Political Economy*, 62, 124-142.

Gould, J. (1972). "Extinction of a Fishery by Commercial Exploitation: A Note." *Journal of Political Economy,* 80, 1031-1039. In Clark, C. (1973) "Profit Maximisation and the Extinction of Animal Species." *Journal of Political Economy*, 81, 950-961.

Gray, L. (1914). "Rent Under the Assumption of Exhaustibility." *Quarterly Journal of Economics, 2*8, 466-489. In Fisher, A. and Peterson, F. (1977). "The Exploitation of Extractive Resources: A Survey." *The Economic Journal,* 87, 681-721.

Gurney,W., Nisbet, R. and Lawton, J. (1983). "The Systematic Formulation of Tractiable Single-Species Models Incorporating Age Structure." *Journal of Animal Ecology,* 52, 479-795.

Hammack, J. and Brown, G. (1974). *Waterfowl and Wetlands: Towards Bio-Economic Analysis.* Baltimore: The John Hopkins Press.

Hardin, G. (1968). "The Tragedy of the Commons." *Science,* 162, 1243-1248.

Hassell, M. (1975). "Density-Dependence in Single Species Populations." *Journal of Animal Ecology,* 44, 283-295

Hearne, J. and Swart, J. (2000). "Modelling: A Tool for Enhancing the Survival Prospects of African Wildlife." *Natural Resource Modelling,* 13(1), 35-55.

Hearne, J., Korrubel, J. and Koch, K. (2000). "Modelling to Optimise Consumptive Use of Game." *Annals of Operations Research,* 95, 269-284.

Hearn, J. (2001). "The Bushmeat Trade is Wiping Out Large African Mammals." *Scientific American,* 284(6), *24-26.*

Hoffman, A. (1989). "Changing Palaeontolgical Views on Mass Extinction Phenomena." In Donovan, S. (Ed.). (1989). *Mass Extinctions: Processes and Evidence* (pp. 1-18). London: Belhaven Press.

Holling, C. (1959). "Some Characteristics of Simple Types of Predation and Parisitism." *Canadian Entomologist,* 91, 385-398.

Hotelling, H. (1931). "The Economics of Exhaustible Resources." *Journal of Political Economy,* 39, 137-175.

Huffman, B. (2002). "The Ultimate Ungulate: Your Guide to the World's Hoofed Mammal Species." (Online) Available: http://www.ultimateungulate.com (2002, January 16).

Hume, D. (1739). "A Treatise on Human Nature." *Hume's Moral and Political Philosophy*. In Perman, R., Ma, Y., McGilvray, J. and Common, M. (1999). *Natural Resource and Environmental Economics (2nd ed.)*. Essex, UK: Longman.

Hume, D. (1751). "An Enquiry Concerning the Principle of Morals." *Hume's Moral and Political Philosophy*. In Perman, R., Ma, Y., McGilvray, J. and Common, M. (1999). *Natural Resource and Environmental Economics (2nd ed.)*. Essex, UK: Longman.

Hutton, J. and Dickson, B. (Eds.). (2000). *Endangered Species Threatened Convention: The Past, Present and Future of CITES*. London: Earthscan.

Huxley, C. (2000)."CITES: The Vision." In Hutton, J. and Dickson, B. (Eds.). (2000). *Endangered Species Threatened Convention: The Past, Present and Future of CITES* (pp. 3-12). London: Earthscan.

International Whaling Commission (2002). (Online) Avaliable: http://www.iwcoffice.org/schedule.htm (2002, January 26).

IUCN. (The World Conservation Union). (2000). "Confirming the Global Extinction Crisis." News Release, Species Survival Commission. (Online) Avaliable: http://iucn.org/redlist/2000/news.html (2001, February 22).

Jablonski, D. (1986). "Causes and Consequences of Mass Extinctions: A Comparative Approach." In Elliot, D (Ed.). (1986). *Dynamics of Extinction*. New York: John Wiley & Sons, 183-229.

Jevons, W. (1865). *The Coal Question (2nd ed.)*. In Fisher, A. (1995). *Environmental and Resource Economics: Selected Essays of Anthony C. Fisher*. Aldershot, UK: Edward Elgar Publishing Company.

Jorgensen, S., Halling-Sorensen, B. and Nielsen, S. (Eds.). (1996). *Handbook of Environmental and Ecological Modelling*. Florida: CRC Press.

Kahn, H., Brown, W. and Martel, L. (1976). *The Next 200 Years*. New York: Morrow.

King, F. (1987). "Thirteen Milestones on the Way to Extinction" In Fitter, R. and Fitter, M. (Eds.). (1987). *The Road to Extinction*. Gland: IUCN.

Kinyua, P., van Kooten, G. and Bulte, E. (2000). "African Wildlife Policy: Protecting Wildlife Herbivores on Private Game Ranches." *European Review of Agricultural Economics,* 27(2), 227-244.

Kiwi Recovery Programme (2002). (Online) Avaliable: http://www.kiwirecovery.org.nz/ (2002, January 16).

Klausmeiser, C. (1998). "Extinction in Multispecies and Spatially Explicit Models of Habitat Destruction." *The American Naturalist,* 152(2), 303-310.

Krebs, C. (1972). *Ecology: The Experimental Analysis of Distribution and Abundance.* New York: Harper Row.

Krohne, D. (2001). *General Ecology (2nd ed.).* Canberra: Brookes/Cole.

Krutilla, J. (1967). "Conservation Reconsidered." *The American Economic Review,* 57, 777-786.

Lamarck, J. (1809). *Philosophie Zoologique.* Paris: Dentu. In Hoffman, A. (1989) "Changing Palaeontolgical Views on Mass Extinction Phenomena." In Donovan, S. (Ed.). *Mass Extinctions: Processes and Evidence* (pp. 1-18) London: Belhaven Press.

Leslie, P. (1945). "On the Use of Matrices in Certain Population Mathematics." *Biometrika,* 33, 183-212.

Leslie, P. (1948). "Some Further Notes on the Use of Matrices in Population Mathematics." *Boimetrika,* 35, 213-245.

Lomborg, B. (2001). T*he Skeptical Environmentalist: Measuring the Real State of the World.* Cambridge, UK: Cambridge University Press.

Lotka, A. (1925). *Elements of Physical Biology.* Baltimore: Williams & Wilkins.

Lovejoy, T. (2002). "Biodiversity: Dismissing the Scientific Progress." *Scientific American,* 286(1), 67-69.

Mace, G. (1995). "Classification of Threatened Species and Its Role in Conservation Planning." In May, R. and Lawton, J. (Eds.). (1995). *Extinction Rates* (pp. 197-213) Oxford, UK: Oxford University Press.

Malthus, T. (1798). *An Essay on the Principle of Population.* In Perman, R., Ma, Y., McGilvray, J. and Common, M. (1999). *Natural Resource and Environmental Economics (2nd ed.).* Essex, UK: Longman.

Mann, C. (1991). "Extinction: Are Ecologists Crying Wolf?" *Science,* 253, 736-738.

Martin, R. (2000)."CITES and the CBD." In Hutton, J. and Dickson, B. (Eds.). (2000). *Endangered Species Threatened Convention: The Past, Present and Future of CITES* (pp. 125-133). London: Earthscan.

May, R., Lawton, J. and Stork, N. (1995). "Assessing Extinction Rates." In May, R. and Lawton, J. (Eds.). (1995). *Extinction Rates* (pp. 1-24). Oxford, UK: Oxford University Press.

McNaughton, S. and Wolf, L. (1979). *General Ecology (2nd ed.).* New York: Holt, Rinehart and Winston.

Meadows, D., Meadows, D., Randers, J. and Behrens, W. (1972). *The Limits to Growth: A Report for the Club of Rome's Project on the Predicament of Mankind.* New York: Universe Books.

Mill, J. (1857). *Principles of Political Economy.* In Perman, R., Ma, Y., McGilvray, J. and Common, M. (1999). *Natural Resource and Environmental Economics (2nd ed.).* Essex, UK: Longman

Mill, J. (1863). *Utilitarianism.* In Perman, R., Ma, Y., McGilvray, J. and Common, M. (1999). *Natural Resource and Environmental Economics (2nd ed.).* Essex, UK: Longman

Mills, M. and Shenk, T. (1992). "Predator-Prey Relationships: The Impact of Lion Predation on Wildebeest and Zebra Populations." *Journal of Animal Ecology,* 61, 693-702.

Milner-Guilland, E. and Mace, R. (1998). *Conservation of Biological Resources.* Oxford: Blackwell Science.

Moran, D. and Pearce, D. (1997). "The Economics of Biodiversity." In Folmer, H. and Tietenberg, T. (Eds.). (1997). *The International Yearbook of Environmental and Resource Economics 1997/1998: A Survey of Current Issues* (pp. 82-113). Cheltenham UK: Edward Elgar Publishing Company.

Murphy, D. (1988). “Challenges to Biological Diversity in Urban Areas”. In Wilson, E. (Ed.). (1988). *Biodiversity* (pp. 29-58). Washington DC.: National Academy Press.

Norgaard, R. (1985). “Environmental Economics: An Evolutionary Critique and a Plea for Pluralism.” *Journal of Environmental Economics and Management,* 12, 382-394.

Norgaard, R. (1989). “The Case for Methodological Pluralism.” *Ecological Economics,* 1, 37-57.

Owen-Smith, R. (1988). *Megaherbivores: The Influence of a Very Large Body on Ecology*. Cambridge, UK: The University of Cambridge Press.

Paine, R. (1966). “Food Web Complexity and Species Diversity.” In Krohne, D. (2001). *General Ecology (2nd ed.).* Canberra: Brookes/Cole.

Paish, F. (1938). “Causes of Changes in Gold Supply.” *Economica,* 5, 379-409.

Panayotou, T. (1992). “The Economics of Environmental Degradation: Problems, Causes and Responses.” In *Green Markets: The Economics of Sustainable Development*. San Francisco: ICS Press for the International Centre for Economic Growth, 1992.

Pearce, D. (1993). *Economic Values and the Natural World.* Cambridge, USA: MIT Press.

Pearce, D. and Moran, D. (1994). *The Economic Value of Biodiversity.* London: Earthscan.

Pearl, R. (1925). *The Biology of Population Growth.* New York: Knopf Publishing Group.

Perman, R., Ma, Y., McGilvray, J. and Common, M. (1999). *Natural Resource and Environmental Economics (2nd ed.).* Essex, UK: Longman.

Pielou, E. (1974). *Population and Community Ecology: Principles and Methods.* New York: Gordon and Breach Science Publishers.

Pimm, S. (1991). *The Balance of Nature? Ecological Issues in the Conservation of Species and Communities*. Chicago: The University of Chicago Press.

Planet Wildebeest. (1997). (Online) Available: http://www.planet-pets.com/plntwldb.htm (2002, February 22).

Pradhan, T. and Chaudhuri, K. (1999). "A Dynamic Reaction Model of a Two-Species Fishery With Taxation As a Control Instrument: A Capital Theoretic Analysis." *Ecological Modelling,* 121, 1-16.

Putman, R. (1994). *Community Ecology.* London: Chapman & Hall.

Ragozin, D. and Brown, G. (1985). "Harvest Policies and Non-market Valuation in a Predator-Prey System." *Journal of Environmental Economics and Management,* 12, 155-68.

Rennie, J., Schneider, S., Holdren, J., Bongaarts, J. and Lovejoy, T. (Eds.). (2002). "Misleading Math About the Earth." *Scientific American*, 286(1), 59-69.

Revenga, C., Brunner, J., Henninger, N., Kassem, K. and Payne, R. (2001). *Pilot Analysis of Global Ecosystems: Freshwater Systems.* Oxford, UK: Oxford University Press.

Ricardo, D. (1817). *Principles of Political Economy and Taxation.* In Perman, R., Ma, Y., McGilvray, J. and Common, M. (1999). *Natural Resource and Environmental Economics (2nd ed.).* Essex, UK: Longman.

Schaefer, M. (1954). "Some Aspects of the Dynamics of Populations Important to the Management of the Commercial Marine Fisheries." *Bulletin: Inter American Tropical Tuna Commission,* 1(2), 25-56.

Schaefer, M. (1957). "Some Considerations of Population Dynamics and Economics in Relation to the Commercial Marine Fisheries." *Journal of Fisheries Research Board Canada,* 14(5), 669-681.

Schaller, G. (1972). *The Serengeti Lion: A Study of Predator-Prey Relations.* Chicago: The University of Chicago Press.

Schoener, T. (1983). "Field Experiments on Interspecific Competition." *The American Naturalist,* 122(2), 240-285.

Simberloff, D. (1992). "Do Species-Area Curves Predict Extinction in Fragmented Forrest?" In Whitmore, T. and Sayer, J. (Eds.). (1992). *Tropical Deforestation and Species Extinction* (pp. 75-90). London: Chapman & Hall.

Simon, J. and Kahn, H. (Eds.). (1984). *The Resourceful Earth: A Response to Global 2000.* Oxford, UK: Blackwell.

Sinclair, A. (1985)."Does Interspecific Competition or Predation Shape the African Ungulate Community?" *Journal of Animal Ecology,* 54, 899-918.

Skonhoft, A. (1998). "Resource Utilisation, Property Rights and Welfare – Wildlife and the Local People." *Ecological Economics*, 26, 67-80.

Skonhoft, A. (1999). "On the Optimal Exploitation of Terrestrial Animal Species." *Environmental and Resource Economics,* 13(1), 45-57.

Smith, A. (1776). *An Inquiry into the Nature and Causes of the Wealth of Nations*. In Edwards-Jones, G., Davies, B. and Hussain, S. (2000). *Ecological Economics.* Oxford, UK: Blackwell Science.

Smith, F., May, R., Pellew, R., Johnson, T. and Walter, K. (1993). "Estimating Extinction Rates." *Nature,* 364, 494-496.

Smith, V. (1969)."On Models of Commercial Fishing." *Journal of Political Economy,* 77, 181-98.

Smith, V. (1975). "The Primitive Hunter Culture: Pleistocene Extinction and the Rise of Agriculture." *Journal of Political Economy,* 83, 727-755.

Solow, R. (1974)."The Economics of Resources or The Resources of Economics." *The American Economic Review*, 64, 1-14.

Stiling, P. (1992). *Introductory Ecology.* New Jersey: Prentice Hall.

Strobele, W. and Wacker, H. (1995). "The Economics of Harvesting Predator-Prey Systems." *Journal of Economics,* 61(1), 65-81.

Swanson, T. (1994). "The Economics of Extinction Revisited and Revised: A Generalised Framework for the Analysis of the Problems of Endangered Species and Biodiversity Losses." *Oxford Economic Papers,* 46, 800-821.

Swanson, T. (1994a). *The International Regulation of Extinction.* London: The MacMillan Press Ltd.

Text of the Convention, Article II: Fundamental Principles (2002). (Online) Available: http://www.cites.org/eng/disc/text.shtml - II (2001, October, 1).

Tietenberg, T. (1992). *Environmental and Natural Resource Economics (3^{rd} ed.).* New York: Harper Collins.

UNEP. (United Nations Environment Program). (2001). "Sustaining Life on Earth." Convention on Biodiversity 2001. (Online) Available: http://www.biodiv.org/doc/publications/guide.asp (2001, December 2).

van Kooten, G., Bulte, E. and Kinyua, P. (1997). "Game Cropping and Wildlife Conservation in Kenya: A Dynamic Simulation Model with Adaptive Control." *Agricultural Systems,* 54(4), 439-462.

van Kooten ,G., Sedjo, R. and Bulte, E. (1999). "Tropical Deforestation: Issues and Policies." In Folmer, H. and Tietenberg, T. (Eds.). (1999). *The International Yearbook of Environmental and Resource Economics 1999/2000: A survey of Current Issues.* Cheltenham, UK: Edward Elgar Publishing Company.

Verhulst, P. (1838). "Notice sur la loi que la population suit dans son accroissement." *Correspondance Mathematique et Physique,* 10, 113-121. In Clark, C. (1976). *Mathematical Bioeconomics: The Optimal Management of Renewable Resources.* New York: John Wiley & Sons.

Volterra, V. (1926). "Variations and Fluctuations of the Number of Individuals in Animal Species Living Together." Reprinted in Chapman, R. (1931). *Animal Ecology.* New York: McGraw-Hill.

Whitmore, T. and Sayer, J. (Eds.). (1992). *Tropical Deforestation and Species Extinction.* London: Chapman & Hal.

Wilson, E. (1988). "The Current State of Biological Diversity." In Wilson, E. (Ed.). (1988). *Biodiversity* (pp. 3-18). Washington DC.: National Academy of Press.

World Resources Institute (Ed.). (1990). *World Resources 1990-1991.* Oxford: Oxford University Press.

World Resources Institute (Ed.). (1992). *World Resources 1992-1993.* Oxford: Oxford University Press.

World Resources Institute (Ed.) (2000). *World Resources 2000-2001.* Oxford: Oxford University Press.