

# TROPHY HUNTING: AN AGE AND SEX STRUCTURED MODEL

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## ABSTRACT

An age and sex structured matrix population model is developed to simulate population dynamics of a trophy hunted polygynous species. The model is used to project population growth rate and abundance of a trophy hunted ungulate species, *Capra falconeri*, found in the western regions of Pakistan. The impact of harvest (hunting) the species on population dynamics is simulated to assess whether a trophy-hunting program, targeting mature adult males, is sustainable. In the context of projected growth rate and projected abundance, the program is found to be sustainable for harvest rates as high as ninety percent of the  $\geq 6$  year old male population. However, other ecological considerations, such as biased sex-ratios, and deterioration in quality of the gene pool prevent such high harvest rates. In view of the sustainability of the program, different delivery mechanisms (or marketing techniques) for sale of hunting permits are assessed to determine the optimal mechanism. In the presence of complete information this turns out to be perfect price discrimination, with a revenue maximizing quota determined by the price elasticity of demand ( $\eta$ ). That is, a larger quota if  $\eta > 1$ , and a smaller quota if  $\eta < 1$ , will maximize revenue. In the more likely scenario of incomplete information however, priority pricing (a form of third degree price discrimination) or second-price sealed bid auctions are found to maximize the seller's expected revenues, as opposed to the existing first-price sealed-bid auction .

## **BIOGRAPHICAL SKETCH**

Ghazi Alam was born in 1976 in Lahore, Pakistan, and is the first of four siblings. He is married to Samar and has two daughters, Dina, aged three, and Rania, aged two.

He obtained his Bachelor of Arts in Economics from the Punjab University in Lahore, Pakistan in 1999. He then went to the Lahore School of Economics, and received a Master of Science in Economics and Finance in 2002.

He worked as an environmental consultant for Hagler Bailly Pakistan, from 2002 to 2006, where he developed an interest and passion for environmental protection and wildlife conservation. Given his academic background, he became interested in the role of economics in achieving conservation objectives.

Ghazi received a Fulbright scholarship in 2006 for graduate study at Cornell University, where he is in the third year of the graduate program in the department of Applied Economics and Management. At Cornell, his academic interests lie in the application of dynamic optimization techniques for optimal natural resource use. He is also interested in wildlife demography, in particular the incorporation of matrix population models into economic models of resource use.

To my children and their generation, and to the hope that my generation leaves a better world for you to experience and enjoy. And to the Markhor, may you flourish, so generations to come may enjoy your beauty and grace.

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## CHAPTER 1

### INTRODUCTION

Humans live off the land and seas, using wild animals, plants, and their products for purposes ranging from food to medicines, shelter, and fiber. In a world that seems intent on liquidating natural resources however, *over-exploitation* has become the second most important threat, after habitat loss and degradation, to the survival of the world's birds, mammals, and plants. *Over-exploitation* involves the *unsustainable* use of the components of biological diversity. The motivations for such use are as varied as the plants and animals that are taken, ranging from subsistence hunting and fishing, to recreational and economic pursuits carried out by wealthy individuals and corporations (Groom et al., 2006).

*Sustainable* use, on the other hand, is defined in Article 2 of the Convention on Biological Diversity (CBD), as “the use of components of biological diversity in a way and at a rate that does not lead to the decline of biological diversity, thereby maintaining its potential to meet the needs of current and future generations” (Multilateral, 1993).

The idea of sustainable use is viewed by some conservationists as an unwelcome challenge, to be avoided by establishing more protected areas and by promoting non-extractive tourism (Soule and Sanjayan, 1998; Kramer et al., 1997). Others however, recognize that such approaches are of little direct value to all but a privileged few, and particularly unjust for the rural poor in many parts of the developing world (Hutton, 2004; Knudsen, 1999). This dichotomy is largely as a result of confusing “preservation” with “conservation”. The two are not the same thing; preservation is an extreme form of conservation - but with no “use” intended (Cooch, 2007). It is essential to recognize that in most cases conservation

will have to be achieved through co-operation in human social space. Thus, the term *incentive-driven conservation* has been suggested for cases where the sustainable use of exploited species generates livelihood benefits that in turn act as the incentives for the delivery of effective conservation (Hutton and Leader-Williams, 2003).

Incentives can take many forms. They may be social or financial. They may be positive or negative, where benefits or penalties, respectively, result from particular actions. In the industrialized world negative incentives based on regulation and enforcement are common, as are positive (and often perverse) incentives based on financial inducements in the form of subsidies or tax breaks. It is important to note that incentives can flow from both extractive and non-extractive uses. In the developed world, the benefits flowing from non-extractive uses, notably tourism and wildlife viewing, are often as significant as those from extractive uses, if not more so.

In the developing world however, the situation is often very different. Here negative incentives are not uncommon, but their successful implementation is more elusive and the state is rarely in a position to provide significant financial inducements for conservation. As a result, successful conservation is forced to rely heavily on the incentives generated by use for a whole raft of reasons often including a lack of accessibility, political stability, infrastructure, and charismatic species (Leader-Williams, 2002; Leader-Williams and Hutton, 2005). Experience with conservation programs has shown that some forms of extractive use, if well managed, properly monitored and based on an understanding of biological limits to sustainable use, can generate significant funds, and provide positive incentives to drive habitat and species conservation. These incentives can take the form of significant livelihood

benefits for the rural poor who live side by side with the exploited species and on whom these species ultimately depend for their continued survival. Furthermore, such forms of use can also be one of the few options for realizing the value of remote or low visibility ecosystems where other forms of tourism are not viable for lack of infrastructure or political stability (Hutton, 2004).

The alternative is unsustainable use and ecological degradation of natural habitats that is all too often associated with deteriorating livelihoods and human welfare.

## **1.1 Trophy Hunting as a Positive Incentive**

One specific form of incentive driven conservation that has gained popularity in recent years is *trophy hunting*, ie, the selective hunting (or harvest) of wild game (usually male) for sport, where the skin, antlers, and/or head are kept as a trophy or memorial. Evidence of revenues generated by the trophy hunting industry in Africa provides economic justification for wildlife as a land use over vast areas (Lindsey et al., 2006). Additionally, trophy hunting has the potential for generating substantial funds that can be used for conservation activities such as habitat protection, law enforcement, and research and monitoring. More importantly, the revenues from trophy hunting are said to provide a strong incentive for conservation and habitat protection by demonstrating the economic worth of wildlife to local people (Shackelton, 2001). Opinion among conservationists concerning trophy hunting however, is polarized, ranging from absolute opposition by protectionists to those who see trophy hunting as a practical means of creating incentives for conservation (Hutton and Leader-Williams, 2003).

Resistance to the idea of killing animals for sport is founded on ethical issues, equity issues in the distribution of hunting revenues, inadequate involvement of communities, corruption, and ecological problems such as setting quotas in the absence of adequate population data, and overshooting of quotas.

Researchers however, have also documented the positive aspects of trophy hunting as a conservation tool including a low off-take rate and a focus on males (typically 2 percent of male populations), both of which do not generally jeopardize wildlife populations, and also mean that trophy hunting can play a role in endangered species conservation (Lindsey et al., 2006). Trophy hunters also tend to pay higher fees per client than conventional tourists (Lewis and Alpert, 1997). Advocates also point out that trophy hunting generates revenues for conservation in areas that may not be suitable for tourism, such as those lacking attractive scenery or high wildlife densities (Leader-Williams and Hutton, 2005). Additionally, trophy hunters may also be less easily dissuaded than conventional tourists from visiting countries experiencing political instability or lack of infrastructure (Leader-Williams and Hutton, 2005). Thus, if properly managed and monitored, it has the potential to ease pressure on wildlife by reducing poaching and preventing conversion of land to agricultural and other uses.

## **1.2 Modeling**

To some degree, it is a fairly recent observation that wildlife is a renewable resource that with management can exist over the long-term. With the advent of “harder science”, managers have increased the sophistication with which they tackle the problem (Eppink and van den Bergh, 2007). The biological theory of sustainable

exploitation is firmly rooted in the field of population ecology, which seeks to understand the responses of populations to increased mortality of individuals through density-dependent compensation. This theory has produced a range of methods and models for estimating sustainable limits of exploitation from simple rules of thumb based on life histories to highly sophisticated models (Groom et al., 2006). These models are usually dynamic, and the simpler models may take the form of linear, logistic, or sigmoid growth functions, among others, that give changes in abundance over time subject to growth and/or density dependent parameters. More sophisticated methods include projections based on matrix, capture mark recapture, or genetic methods.

The study of population dynamics is, in simplest terms, the study of changes in abundance ( $N$ ). In other words, population dynamics is the study of  $\Delta N$ . Further, change in abundance is simply the difference between the number of individuals entering a population and those leaving a population.  $\Delta N = \text{“births”} - \text{“deaths”}$ . Whenever the number of additions is greater than the number of departures then  $\Delta N$  will be greater than 0, (ie, the population grows). Arrivals can mean new births or immigration into the population. Departures can be by means of death and emigration. Thus,  $\Delta N = (\text{“births”} + \text{“immigrants”}) - (\text{“deaths”} + \text{“emigrants”})$ . Population dynamics is more or less defined by this equation.

Most studies using dynamic models include only one sex, usually the female, under the assumptions that the sexes are identical or that the population dynamics are determined by one sex only. Sexual dimorphism in vital rates, such as mortality, age to maturity, and fecundity is well documented in many species; neither assumption therefore is generally valid. Two-sex population projection models were proposed as long ago as 1986 by Caswell and Weeks (Caswell and Weeks,

1986). To the extent that both males and females are required for reproduction, population demography is nonlinear. Very few studies have used two-sex models explicitly since they were first proposed however, primarily due to a lack of detailed information required by such models. According to Rankin and Kokko (2007), males can have a diverse range of effects on models of population density, thus the importance of males is not limited to only conservation action, but also to pest control and management of invasive species. Additionally, though one-sex models of population dynamics are highly competent at describing population dynamics, Rankin and Kokko (2007) state that we can expect surprising deviations from those predicted if male dependence of population dynamics has not been incorporated in the dynamical explanation. They go on to state that “empirically derived graphs depicting changes in population growth (or more explicitly still, changes in the numbers of females and males separately) at various male and female densities would be a welcome sight in the literature”. As a result, rather than just looking at per female productivity, Rankin and Kokko (2007) strongly advocate investigating the role of males on population dynamics in a population setting.

Furthermore, incorporating economics in such models is imperative to make them politically acceptable. Economists are pre-eminently equipped to analyze this issue, but only if they incorporate appropriate biological indicators and related ecological theories in their models (Eppink and van den Bergh, 2007). Economic models with a biological component are frequently referred to as bio-economic models, and fall in to four main categories, ie, cost-effectiveness, macroeconomic growth, general equilibrium, and renewable resource models. Criticisms, from a biological perspective, of bio-economic models generally refer to oversimplification of biological processes. Failure to account for ecological complexity therefore, is



said to bias conclusions in favor of political or economic objectives.

It is easy to recommend incorporating more ecological complexity in bio-economic models, but is fair to add a disadvantage; namely that theoretical, analytical solutions will often become impossible. Fortunately, numerical solutions will always be possible. Milner et al. (2007) suggest that in order to make firmer predictions about the effects on population growth and viability, both large-scale empirical manipulations of harvesting regimes and theoretical studies, including simulation modeling, are urgently needed. It has been suggested that perhaps this is the way the go for this type of research, since there is a trade-off between ecological relevance and analytical tractability (Eppink and van den Bergh, 2007).

### **1.3 Delivery Mechanism**

In Pakistan, a central authority (the National Council for the Conservation of Wildlife), determines annual quota allocations of hunting permits, for areas in which the Markhor is found. The existing quota for the population in Balochistan is five, which is an increase, based on increased population numbers, from just two in years before 2004. Once the quota is allocated, the provincial wildlife department issues a call for sealed-bids for the permits by advertising in national and international newspapers. The reservation price (the price below which a permit will not be sold) is currently set at USD50,000, an increase, based on higher perceived demand, from USD25,000 before 2006.

The hunts are usually arranged by a local outfitter, who arranges the hunter's acquisition of the permit (the hunter has to be present in person to actually receive the permit however), local travel and accommodations, trackers and guides, and

the export license if the hunt is successful. If the hunt is unsuccessful because of the absence of a trophy she is given the option of a refund or a return visit the following year. If however the hunt is unsuccessful because she missed his shot, she is not refunded the money.

The existing delivery mechanism for the sale of permits is a first-price sealed-bid auction.

## 1.4 Objectives

The main objective of this paper is to model and simulate two-sex population dynamics with harvest in order to assess the conditions under which harvest might be biologically sustainable. To do this, a detailed matrix population growth model (based on methods developed by Leslie, Lotka, Volterra, and most recently by Caswell (Caswell, 2001)) is formulated that can track and project the population (abundance) into the future accounting for positive and negative shocks such as harvesting.

An very simple economic component is then added to this model to link quota allocation decisions, derived assuming third-degree monopoly pricing (perfectly discriminating monopolist), to species numbers and growth rates. In addition, to this simple economic analysis, recommendations on the optimal marketing scheme<sup>1</sup> (or delivery mechanism) for sale of hunting permits are made.

The main questions I hope to answer are:

1. Are current recommendations of a 2 to 5 percent offtake biologically sustain-

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<sup>1</sup>Defined as one which maximizes the seller's expected revenues.

able?

2. Is targeting a specific age or sex class biologically sustainable?
3. What combination of permit price and quota allocation maximizes revenue, and under what conditions?
4. What is the optimal delivery mechanism for the sale of hunting permits?

It is hoped that the methods and model developed in this paper may be used by planners and managers as a framework to make quota allocation decisions, and market them using optimal delivery mechanism, while maintaining sustainable harvest programs. It is also hoped, in light of the research and recommendations of Rankin and Kokko (2007), that the model developed here and the results of the simulation can be applied more generally to study the dynamics of other species for which “males matter”, particularly when thinking about conservation or biological control programmes.

It is important to note that this paper is not a comment on the ethics or even a justification for trophy hunting. It is however, a recognition of a practice that exists in many parts of the world and is therefore, an attempt at contributing to its scientific foundations, in addition to adding to the literature on two-sex population dynamics.

## 1.5 Organization

Chapter 2 reviews literature related to trophy hunting and the use of bio-economic models. In addition, some of the two-sex matrix population projection literature is also reviewed.

Chapter 3 then presents the development of the actual model. It begins with explaining the formulation of projection matrices from a basic life cycle graph (LCG), before delving in to more complex two-sex matrix models. The chapter ends with development of a two-sex matrix population model for a species subjected to harvest. A linear demand function relating permit prices to numbers of permits issued (in effect quotas for harvest) is also incorporated to study the revenues generated under various harvest scenarios.

Chapter 4 then demonstrates the use of the model as it applies to a trophy hunted species of Markhor (*Capra falconeri*) in Pakistan.

Chapter 5 reviews literature related to auction theory and monopoly pricing in the context of the existing delivery mechanism. After assessing whether the first-price sealed bid auction is optimal, it concludes that it is not and ends with recommendations for alternate delivery mechanisms that are optimal.

The thesis ends with conclusions in chapter 6.

## CHAPTER 2

### LITERATURE REVIEW

#### 2.1 Trophy Hunting

Commercial and sport hunting are economically significant activities in many developed countries. 33,000 jobs in the United Kingdom depend on hunting for example. Sealing and whaling used to provide jobs for Norwegian and Canadian mariners and hunters, who suffered economic loss when these activities were banned. In New-Zealand, recreational hunting and trout and big game fishing generate several thousand full and part-time jobs, and possum hunting and trapping used to be economically significant in some areas before the successful campaign against fur in Europe and North America. However, the economies of rich countries do not depend significantly on hunting and if it was banned, recreational hunters would simply switch their discretionary spending, thus creating jobs in other sectors of the economy.

The situation is quite different in poorer countries, where wildlife has always been used as a resource and “Use or non-use is not the issue; sustainable use is” (Gunn, 2001). The colonial powers, after reducing many species to rarity or extinction, generally adopted policies of strict preservation of wildlife. This was done without regard to the needs of local people who were regarded as poachers even when they engaged in traditional subsistence hunting. Less attention is given to the fact that they have few, if any, alternative options to using the available wild resources. The forced abandonment of homes and fields because crops are destroyed by wildlife adds further strain to the relationship between people and wildlife (see Gunn, 2001; MacDonald, 2005; Knudsen, 1999).

Trophy hunting as it exists today is largely an international activity. This internationalization of hunting does not happen without a demand for hunting opportunities on the part of wealthy foreign hunters, a demand grounded, at least in part, in the rise of environmentalism and conceptions of public good that challenge the activities of hunters closer to home. In North America, for example, participation in hunting has declined over the past 25 years. The reasons for this are multiple but can be loosely tied to a rising appreciation of the rights of non-human species. International trophy hunting, however, is on the increase, and this is reflected in a 71 per cent increase in the importation of foreign game killed by US trophy hunters since 1990 (MacDonald, 2005). No doubt this is fueled by exoticism and the status derived from the sanctioned rewards of the hunting community, but it is partially also a flight from opposition. As trophy hunting faces increased opposition in North America and Europe, and as opportunities to hunt encounter increased restrictions, hunters, like multinational industries, flee to grounds where they can escape those restrictive conditions.

From a “community” perspective, at least one motivation for them to participate in trophy hunting programs is the chance to acquire the cash through which they may realize the long-promised material benefits of development. In essence, the implementation of sport trophy hunting provides the means for converting wildlife to a commodity with exchange value outside the community. Wildlife, then, becomes a source of direct income that can be used to acquire some desired benefits such as increased household income and the development of infrastructure. It is the promise of these benefits that is meant to provide villagers with a disincentive to engage in hunting. Increased household income or the benefits of social or physical infrastructure are taken as a measure of increased development so that wildlife, as commodity, becomes one basis of community development. Of

course, this logic is grounded in inequity, and only works where there is a vast difference in the material conditions of those providing access to wildlife and those paying for the experience of the hunt (MacDonald, 2005).

### **2.1.1 Positive Aspects**

Poor countries gain considerable revenue from trophy hunting. The impoverished Mongolian government used to charge \$10,000 for a permit to shoot a snow leopard before its hunting was banned, and a 16-day hunt with one snow leopard used to cost \$25,000 per person; any wolves shot along the way were thrown in for \$600. Bulgarian dealers sell falcons in the West for \$10,000. Orangutan were sold in Taiwan in the 1980s at \$30,000 each, though the local traders in Indonesia received less than \$200 each for them still a very considerable sum by local standards (Gunn, 2001). None of these cases is part of a sustainable management program, but other countries which manage their wildlife effectively have achieved substantial revenues from trophy hunting while maintaining or increasing their wildlife populations.

Perhaps the largest scale on which trophy hunting is practiced is in the African continent. During the 1980s and 1990s, the potential for trophy hunting revenues to promote conservation was increasingly acknowledged (Lindsey et al., 2007). In several African countries, there was a gradual alignment of trophy hunting industries with conservation and development policies, supported by a number of international donor agencies. This happened first in southern Africa (eg, as part of the Communal Areas Management Programme for Indigenous Resources (CAMPFIRE) program in Zimbabwe and Administrative Management Design program in Zambia), then in Central Africa (eg, through the Programme de Développement des Zones de Chasse Villageoise in Central African Republic and Zones d'Intérêt Cyn-

gtique Gestion Communautaire in Cameroon), and more recently in West Africa (eg, through Gestion Participative des Ressources Naturelles et de la Faune, and Ecosystemes Protgés d'Afrique Soudano-Sahlienne).

Lindsey et al. (2007) provide a review of the scale of the African trophy hunting industry, and assess both positive and negative issues relating to hunting and conservation in Africa. Trophy hunting occurs in 23 countries in Africa, with the largest industries occurring in southern Africa and Tanzania, where the industry is expanding. Using the most recent estimates for the countries with significant hunting industries, where estimates are available, Lindsey et al. (2007) estimate that trophy hunting generates gross revenues of at least US \$201 million per year in sub-Saharan Africa: from a minimum of 18,500 clients (see Lindsey et al., 2007, Table 1). Over 1,394,000 square kilometers is used for hunting in sub-Saharan Africa, exceeding the area encompassed by national parks by 22 percent in the countries where hunting is permitted.

Country specific examples of trophy hunting programs include that of Tanzania for which hunting licenses alone yielded \$4.5 million in 1990. Sports hunters who wish to hunt lion in Tanzania are required to stay for 21 days and on average spent \$35,000. Before Kenya imposed a ban on hunting, the total revenue from sport hunting contributed about 6.5 percent to the total foreign exchange from tourism. At Phinda Izilwane Park in Kwa-Zulu, South Africa, hunters pay \$30,000 to shoot a white rhino. In Malawi, rural communities derive 2.5 times more cash from wildlife than the market value of their subsistence agricultural products (Gunn, 2001).

Perhaps one of the most well known trophy hunting programs is the CAMP-FIRE program in Zimbabwe, which was set up by the Zimbabwean Department of



National Parks and Wildlife Management in 1986, with the support of the World-wide Fund for Nature, the Office of USAID, Harare, and the Centre for Applied Social Sciences at the University of Zimbabwe. Over five million people almost half the population live in communal areas, which make up 42 percent of the country. Communities may decide to participate in CAMPFIRE, which around half had done in August 1996.

In 1995, CAMPFIRE generated \$2.5 million, a substantial sum given that game wardens are paid as little as \$80 per month. This revenue is gained from hunting safaris, tourism such as photographic safaris, sales of products such as animal products and crocodile eggs (for sale to crocodile farmers), and rafting licenses. Around 90 percent of the revenue is generated from the sale of big game hunting licenses, and 64 percent of this is derived from elephant trophy hunting licenses which in March 1996 cost \$9,000. Over the period 1989-93, 22 percent of revenue was reinvested in wildlife management and 54 percent devolved to the participating communities on the communal lands. Communities spent their shares on infrastructure development such as water supply, clinic and school development, farm fencing (to keep out crop-destroying elephants, hippos, buffalo, and kudu) and roading, income generating projects, and cash distributions to families for their own use. In some areas, this income amounts to 50 percent of a household's annual income and enables families to pay for items such as school fees.

Masoka Ward, a formerly impoverished area, earned \$100,000 in 1994 from a safari hunting concession organized through CAMPFIRE. The ward used the money to build a health clinic, pay game guards, and fund a football team, and each of the 140 households also received more than four times their annual income for drought relief, either in cash or maize. This revenue, of course, would not be

available without the sale of hunting licences. It would be even greater were it not for the ban on international trade in elephant products under the Convention on International Trade in Endangered Species and their Products (CITES) since 1990 (Gunn, 2001).

Whereas the total population of African elephants fell by half between 1975 and 1990 (from 160,000 to 16,000 in Kenya), Zimbabwe's elephants have increased steadily-32,000 in 1960, 52,000 in 1989, and over 70, 000 in 1993. Though more recent estimates are not available due to the political and security situation in the country, it is thought that the population has continued to grow since then. The national trophy off-take is restricted to no more than 0.7 percent per year, which is clearly sustainable. Because they have a stake in sustaining populations of economically valuable game animals, Zimbabweans have a commitment to conservation. As a result, species such as elephants which are rare or extinct in many other countries are thriving in Zimbabwe, along with populations of other animals which benefit from protection of big game habitat (Gunn, 2001).

In Pakistan trophy hunting in its present form is a collection of several such hunting programs that were initially started independently of each other (importantly they were not initially community based) and brought under the community based trophy hunting program umbrella in 1999. The earliest instance was launched by the NWFP Wildlife Department in 1983 as the 'Chitral Conservation Hunting Program', a trophy-hunting program for Markhor. The program lasted eight years until the government banned the export of trophies along with all big game hunting throughout Pakistan in 1991. From 1983 to 1991, hunters from Safari Club International paid a total of \$250,000 in trophy fees, which were deposited in a special account of the NWFP Wildlife Department for a while and

later deposited in the national exchequer. The program was revived in 1995 as part of the Community Based Trophy Hunting Program, where a conservative 2 percent of males older than 6 years are harvested, and has generated \$0.8 million in revenue since then. The longest running purely Community Based Trophy Hunting Program is the Torghar Conservation Project (TCP) established in 1984. This project was initiated by the tribal leaders in the Torghar Hills of Baluchistan province with the help of wildlife biologists from the US Fish and Wildlife Service. In 1994, TCP was formalized as a registered NGO - the Society for Torghar Environmental Protection (STEP), and until 2000 had generated over \$1 million in revenue (Frisina, 2000).

Lindsey et al. (2007) also cite numerous other studies which show that where well managed (as in some southern African states), trophy hunting involves low off-takes and is sustainable. Low off-takes and high prices mean that trophy hunting can play a role in creating incentives for the conservation of threatened and endangered species. Trophy hunters pay higher fees per client than conventional tourists and so revenues can be generated from lower volumes of people, resulting in potentially lower environmental impacts (Lewis and Alpert, 1997). Significantly, trophy hunting generates revenues for conservation in areas which may not be suitable for tourism, including some countries experiencing political instability. Lindsey et al. (2007) conclude that trophy hunting is therefore, of major importance to conservation in Africa by creating economic incentives for conservation over vast areas, including areas which may be unsuitable for alternative wildlife-based land uses such as photographic eco-tourism (see Lindsey et al., 2006, 2007; Hutton and Leader-Williams, 2003; Hutton, 2004; Knudsen, 1999).

### 2.1.2 Negative Aspects

There are, however, a number of well publicized problems associated with trophy hunting which limit the extent to which the industry contributes to conservation objectives. These include ethical, biological and social problems (Lindsey et al., 2006). Meanwhile, animal rights and welfare groups oppose hunting due to a fundamental rejection of the concept of killing animals for sport (Lindsey et al. (2007); Gunn (2001)). Discussion concerning trophy hunting is polarized, with animal rights groups and protectionists on one side, and hunters and pragmatic conservationists on the other (Hutton and Leader-Williams, 2003; Lindsey et al., 2007). This polarisation is exacerbated by a lack of reliable data on the impact of trophy hunting on wildlife conservation. Most information on trophy hunting occurs in unpublished grey literature, and discussion of hunting in the popular media is sometimes emotive. Lindsey et al. (2006) also report that “in South African game ranching areas, the high value of wildlife as trophies has encouraged the division of large areas into small blocks surrounded by *game-proof*, where *non-huntable* predators are persecuted because they prey on trophy species”.

Lately, the negative evolutionary consequences of trophy hunting have also begun to be documented. Some researchers (Coltman et al., 2003; Whitfield, 2003) report that horn sizes and body weight of a certain species of ungulate has decreased over the years because hunters have targeted the largest trophies they could find. But scientists carrying out these studies did not call for a cessation of hunting; instead they recommended a change in regulations to prevent hunters taking the largest animals. Shackelton (2001) states “evidence suggests that in the short term, there are few if any negative effects of trophy hunting. This is to be expected, at least where the majority of mature males are not hunted. What is

unknown however, is the long-term genetic impact of this activity, because trophy hunting removes what are most probably the genetically superior individuals from a population". Again, the impact will likely be minimized if only a fraction of the mature trophy males are taken each year. Shackelton does admit however, that there is no data to support this supposition.

Conclusions on the demographic side effects of trophy hunting are equivocal. (Singer and Zeigenfuss, 2002) for example, report that horn size and mating behavior have no effect on survivorship except in heavily hunted populations. For hunted rams at least they also concluded that trophy hunting decreased competition between rams for obtaining copulations, and likely altered dominance hierarchies of rams, natural selection for largest-horned rams, and potentially the genetic composition of populations. Trophy hunting might select for phenotypes of largest-horned rams, and those largest-horned rams may have higher heterozygosity or specific genetic backgrounds that contribute to more rapid rates of horn growth. Conversely, trophy hunting permits more subdominant and smaller-horned rams to obtain copulations, and thus may increase the ratio of effective population size to census population size and thus increase total genetic diversity.

Milner et al. (2007) also report on the demographic side effects of trophy hunting and conclude that though the mechanisms by which selective harvesting could affect population demography are relatively well documented, the extent to which they affect population growth is still poorly understood. However, because many of these effects are likely to act additively, they may nonetheless reduce the population growth rate more than first anticipated. Milner et al. (2007) suggest that though good estimates are lacking for many parameters, conceptual models would be helpful in assessing when demographic side effects might start to limit popula-

tion growth and in guiding empirical data collection.

As the world’s population continues to grow, and habitat shrinks, pressure on wildlife will increase. Inhabitants of developing countries, like Western environmentalists, are entitled to a materially adequate standard of life. They cannot and should not be expected to protect wildlife if it is against their interests to do so. The only feasible strategy to protect the interests of both wildlife and people is one that integrates conservation and development, as in Zimbabwe. Gunn (2001) states that “whatever we may think of trophy hunting, at present it is a necessary part of wildlife conservation in many parts of the world”.

## **2.2 Bio-economic Models**

Models are important tools in the development of management recommendations for the sustainable use and conservation of biodiversity (in short biodiversity management). They are used both in ecological and economic research. In ecology, models are used to analyze how biodiversity management affects the dynamics and functioning of ecosystems. However, the usefulness of these models for policy advice is limited, because they do not address the socioeconomic dimensions of the problem, including economic, institutional, and political aspects. These issues are actual topics of economic research and modeling. Many economic models are, however, also deficient, when they contain oversimplified assumptions on the ecological effects of conservation or do not represent current ecological knowledge. The observation that disciplinary models exhibit complementary limitations leads to the simple conclusion that it is beneficial to merge ecological and economic knowledge via ecologicaleconomic models (Watzold and Drechsler, 2007).

Recently, Eppink and van den Bergh (2007) evaluated how well environmental-economic models describe biodiversity loss and conservation issues. Four types of economic models turn out to dominate economic research into biodiversity conservation: cost-effectiveness models, renewable resource extraction models, macroeconomic growth models with natural resources, and general equilibrium models with natural resource externalities. Eppink and van den Bergh (2007) assessed the advantages and disadvantages of each modeling approach and presented recommendations for improvement. Their analysis however, was based on biodiversity as a whole and not on specific species, for which the renewable resource extraction models outperform the other three.

Renewable resource extraction models reflect that a species' population may have economic value, particularly when harvested. This idea was first applied to fisheries (Gordon, 1954; Schaefer, 1954). Clark (1973) extended and popularized its use and showed that extinction is optimal if a species is unable to generate a competitive return that is determined by economic and biological parameters (see also Clark and Munro, 1975). The Clark (1973) model, and the extensions provided in Clark et al. (1979) and in Conrad (1999) illustrate an approach for deriving sustainable harvesting rates, with the latter utilizing a spreadsheet modeling approach.

Johannesen (2006) presents a bioeconomic model in order to compare the performance of an ICDP based on a link between the benefit transfers and the conservation objective, with an ICDP based on unconditional transfers. The model however, is static and involves one agent, namely the local people. Hence, the model analyses solely how the local people respond to ICDP benefits, and ignores any dynamic interaction between the local people, the ICDP manager, and the

wildlife species.

Bulte (2003) focuses on differences between poaching and conservation of different species. Bulte and Horan (2003) develop a model of open-access wildlife exploitation, habitat conservation, and agriculture, in which farmers may either hunt for wildlife or grow crops. They show that increasing wildlife conservation may well be pareto-superior to equilibria in which agriculture dominates. Kinyua et al. (2000) also deal with wildlife management but focus more on the competition between wildlife and grazing and, in particular, on the incentives for large commercial ranchers.

Skonhøft (1998) considered the impact of different property-sharing regimes on the incentives of the park manager and on the welfare of the communities. He modeled a single interaction between wildlife and the community, in the form of intrusions; the park manager's incentives derived from the relative marginal values of tourism and hunting. Johannesen and Skonhøft (2005) present a nash game in which both the communities and the park manager choose harvesting effort, as opposed to off-take, in a form of duopoly competition. Within a Gordon-Schfer-type model, their paper focuses on the strategic interaction between the manager of a protected area and a group of local people living near the park. The park manager benefits from wildlife through non-consumptive tourism and safari hunting and local people benefit through hunting but they also bear costs as wildlife causes agricultural damage. Depending on the economic and ecological environment, they show that ICDPs relying on money transfers to the local people derived from the park manager's activities may or may not promote wildlife conservation and the effects on the welfare of the local people are ambiguous.

Analysing structured wildlife harvesting models, ie, models where the species



is grouped in different classes according to age and sex, has a long tradition within biology. Caswell (2001) gives a recent in-depth overview (see also Getz and Haigh, 1989). However, economic analysis plays only a minor role in these books. Economic analysis is introduced more explicitly in Cooper (1993) who formulates a simulation model that finds the economically optimal level of deer tags for hunting zones and where the deer population is structured in bucks and does.

Skonhøft et al. (2002) analyze various management strategies for a mountain ungulate living in a protected area and a hunting area. Clark and Tait (1982) who studied the optimal harvest value in a sex selective harvesting model and where the population hence was grouped in two stages, meat value maximisation. See also the two stage seal model in Conrad and Bjørndal (1991).

Also relevant to my research is the growing literature on the optimal management of multi-use species, in which wildlife is both a resource and a pest, such as Zivin, Hueth, and Zilberman (Zivin et al.), Rondeau (2001), and Rondeau and Conrad (2003). Most recently, Horan and Bulte (2004) consider optimal management in the presence of second-best trade restrictions. They found the shadow value of wildlife to the community may be negative or positive, which can create certain complications. The focus on optimal wildlife management by a single planner is obviously appropriate for the case of private landowners in North America (struggling with migrating beavers or feral pigs) or local governments trying to deal with an exploding deer population. But the set-up may be less applicable to the context of developing countries where nuisance species often pose greater burdens upon farmers than in developed countries, and where property rights to many wildlife species are typically imperfectly enforced.

Recently, there has been a strong emphasis on bio-economic models with spatial

distribution as a key element, in most instances formulated within the context of marine reserves (Conrad, 1999; Sanchirico and Wilen, 2005). These models have, among others, analyzed under what ecological and economic conditions, and to what extent, marine reserve creation may increase aggregate biomass and change the profitability of a fishery. A somewhat different type of study is Skonhøft et al. (2002), who analyze the optimal management of a chamois population moving between a protected area and a surrounding hunting area.

Perhaps the most relevant article for my research is that by Bradshaw and Brook (2007), who analyze the ecological and economic costs/benefits of a series of potential harvest management options for Australia's banteng (*Bos javanicus*) population, with the aim being either to: (1) maximize sustainable yield (MSY); (2) maximize harvest of trophy males; (3) maximize indigenous off-take; (4) suppress density or completely eradicate the population; (5) minimize risk of extinction whilst limiting range expansion; (6) scenarios incorporating two or more of options. Their modeling framework employed stochastic, density-regulated two-sex matrix population models. For each management option, they present a simple economic analysis that incorporates estimated costs of management implementation and associated profits projected. Results demonstrate that revenues of >AU\$200,000 is possible from meat production and safari hunting without compromising long-term population stability or the conservation status of this endangered bovid.

### **2.2.1 Two-sex Dynamics**

The majority of population dynamical models only view the population from the female point of view (Caswell, 2001). This assumption makes life rather simple, and allows for mathematical tractability in more complicated models of populations.

The logic behind the assumption is that males will be born and die at the same rate as females. This means that the sex ratio is always even, and the female density therefore constitutes half of the total population density. The assumptions used in single-sex models hold under limited conditions, where models assume that male availability does not limit female reproduction, the sex-ratio is even, and male life history does not differ from that of females (Caswell and Weeks, 1986; Lindstrom and Kokko, 1998). If such assumptions are fulfilled, a model incorporating two sexes will always produce a total population that is twice the number of females, rendering the explicit incorporation of males unnecessary. If the presence and behavior of males does have a discernible influence on population equilibria or stability, one-sex population models should be abandoned in favor of two-sex models, particularly when thinking about conservation or biological control programmes. It is now increasingly recognized that the presence and behavior of males may matter to population processes.

Rankin and Kokko (2007) ask the question of whether males matter to population dynamics, operationally defined as a dependency of population growth on the relative density of males. They provide simple models, and evaluate the current empirical evidence for them, that illustrate various mechanisms of such male influence: mate searching behavior, male resource use (including effects of sexual dimorphism), sexual harassment and sexual segregation. In each case, theory predicts that males can have an effect on population densities, and in some extreme cases a positive feedback between an increasingly male-biased sex ratio and female harassment may theoretically even bring about population extinction. Deviations from monogamy often mean that sexual reproduction can destabilize dynamics rather than stabilize it (Caswell and Weeks, 1986; Lindstrom and Kokko, 1998). Unstable dynamics generally occur at high growth rates, and the mixed results on

stability make sense in the light of the results in Rankin and Kokko (2007): they generally find that various aspects of male behavior can either promote or hinder population growth. The results of their study, and the literature reviewed, show that the males can have a substantial effect on population dynamics, particularly so when human influences result in biased sex ratios (Rankin and Kokko, 2007).

## CHAPTER 3

### BIOECONOMIC MODEL

#### 3.1 The Life Cycle

Rates of birth, growth, maturation, fertility, and mortality describe the movement of individuals of a species through the life cycle, and are called vital rates (Caswell, 2001). The life cycle is a fundamental unit of description of this process, and a graphical description of the life cycle is appropriately called a *life cycle graph* (LCG). The construction of an LCG proceeds as follows:

1. Choose a set of stages (ie, *i*-states) in terms of which to describe the life cycle (these could be stages, age-classes etc).
2. Choose a *projection interval*, defining the time step in the model. The structure of the graph and the resulting matrix depends on whether the time interval  $(t, t + 1)$  represents a day, a week, a year, etc.
3. Create a *node* for each stage; number the nodes from 1 through  $s$ . The order of the numbering is irrelevant but it is convenient to assign the number 1 to a stage representing newborn individuals. The symbol  $N_i$  denotes node  $i$ .
4. Put a directed line or *arc* from  $N_i$  to  $N_j$  if an individual in stage  $i$  at time  $t$  can contribute individuals (by development or reproduction) to stage  $j$  at time  $t + 1$ . If an individual in stage  $i$  at time  $t$  can contribute to stage  $i$  at  $t+1$  (eg, by remaining in the same stage from one time to the next), put an arc from  $N_i$  to itself; such an arc is called a self loop.
5. Label each arc by a coefficient; coefficient  $a_{ij}$  on the arc from  $N_i$  to  $N_j$  gives the number of individuals in stage  $j$  at time  $t+1$  per individual in stage  $i$  at

time  $t$ . Thus,

$$n_i(t+1) = \sum_{j=1}^s a_{ij} n_j(t) \quad (3.1)$$

Those coefficients may be transition probabilities or reproductive output.

A simple example of an LCG is given in figure 3.1.

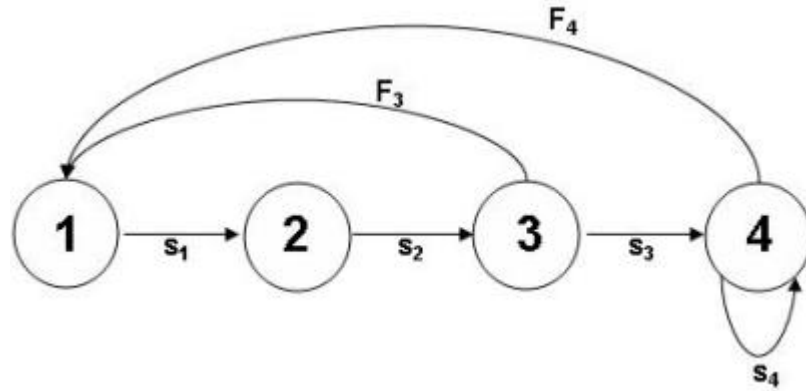


Figure 3.1: A Simple Life Cycle Graph

### 3.2 Dynamic Matrix Population Models

Studying the life cycle in a demographic context requires a way to translate from the individual to the population level, and matrix population models provide such a link. There are two simple rules for converting an LCG to matrix form:

1. If the life-cycle diagram has  $s$  nodes, then the corresponding projection matrix is a  $(s \times s)$  dimension square matrix.
2. If an arc connects node  $i$  to node  $j$  (where the direction of the arc is from  $i$  to  $j$ ), then the value of this arc corresponds to the  $a_{j,i}$  element of the projection

matrix  $\mathbf{A}$ . If there are  $n$  directed arcs in the life-cycle diagram, then there will be  $n$  and only  $n$  non-zero elements of the projection matrix

Then, the LCG in figure 3.1 will translate to a  $4 \times 4$  *Projection* matrix (equation 3.2) with six non-zero elements:

$$\mathbf{A} = \begin{pmatrix} 0 & 0 & F_3 & F_4 \\ s_1 & 0 & 0 & 0 \\ 0 & s_2 & 0 & 0 \\ 0 & 0 & s_3 & s_4 \end{pmatrix} \quad (3.2)$$

A projection matrix describes the probabilities of making a transition between now and next year (or whatever the projection interval is). In other words, the probability of moving from (or contributing to) a class of individuals now, to the another class of individuals next time step. We can see this visually by picturing each column of the matrix as a from state (ie, individuals will move from or contribute from a given age class) at time ( $t$ ). The rows are the age classes at the next time step ( $t+1$ ), to which individuals are contributed. So, each column is an age class now, and each row is an age class next time step. The projection matrix connects the different age classes at each of the 2 time steps. All one needs to do is ask, what is or are the contributions of a particular age class now to a given age class next year. If there is a contribution, then this is a non-zero element in the matrix. If there is no connection, then the corresponding matrix element is 0. This basic idea is shown schematically in figure 3.2:

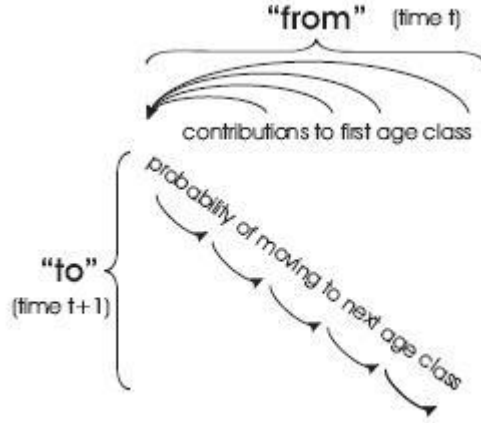


Figure 3.2: Schematic of a Projection Matrix

So, the fertility row consists of contributions from individuals in a particular age class now to the first age class (babies, for models based on a post-breeding census, and one year olds for a pre-breeding census). The diagonal is the probability of moving to the next age class. All of the other elements are 0, because there is no connection between these age classes.

In matrix notation this may be written as:

$$\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t) \quad (3.3)$$

Thus, for our example:

$$\mathbf{n}(t+1) = \begin{pmatrix} 0 & 0 & F_3 & F_4 \\ s_1 & 0 & 0 & 0 \\ 0 & s_2 & 0 & 0 \\ 0 & 0 & s_3 & s_4 \end{pmatrix} \begin{pmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \end{pmatrix} \quad (3.4)$$



The dominant eigenvalue of the projection matrix indicates the rate of population change through time (Caswell, 2001), and by convention is denoted by  $\lambda$ .

### 3.3 Two-Sex Models

Most dynamic models include only one sex, usually the female, under the assumptions that the sexes are identical or that the population dynamics are determined by one sex only (eg, *female dominance*: that population dynamics are determined by the female vital rates and there are always enough males to fertilize all the females). Sexual dimorphism in vital rates, such as mortality, age to maturity, and fecundity is well documented in many species; neither assumption therefore is generally valid. Demographic sex differences are most pronounced in polygynous species, where sexual selection has molded the mating system such that small or otherwise frail males have little chance for conveying genes to the next generation. Sexual size dimorphism is frequently pushed so far that males have higher mortality risk than females either as juveniles, in adulthood, or both (Lindstrom and Kokko, 1998; Loison et al., 1999).

Caswell (2001) states that sexual dimorphism and the failure of the dominance assumption necessitates the inclusion of both sexes in a population projection model. Consequently, the model is nonlinear because only in a nonlinear model can reproduction depend on the relative abundance of the sexes (Caswell, 2001). Despite the substantial research on the evolution of sexual reproduction, there exist relatively few studies that focus on the consequences of sexual reproduction or its inclusion in single species population dynamics. This is, to some extent, at

odds with the knowledge of the complex dynamics displayed by nonlinear systems elsewhere (Lindstrom and Kokko, 1998). In their most basic form, two-sex models differ from density-dependent models in that the vital rates depend only on the relative, not the absolute, abundances of stages in the population (they are sometimes called frequency-dependent for this reason). Such models are necessarily non-linear (Caswell, 2001).

A simple two-sex LCG is shown in figure 3.3 below. The LCG as depicted is in z-transformed or reduced form (see Caswell, 2001, chapter 4, chapter 15).

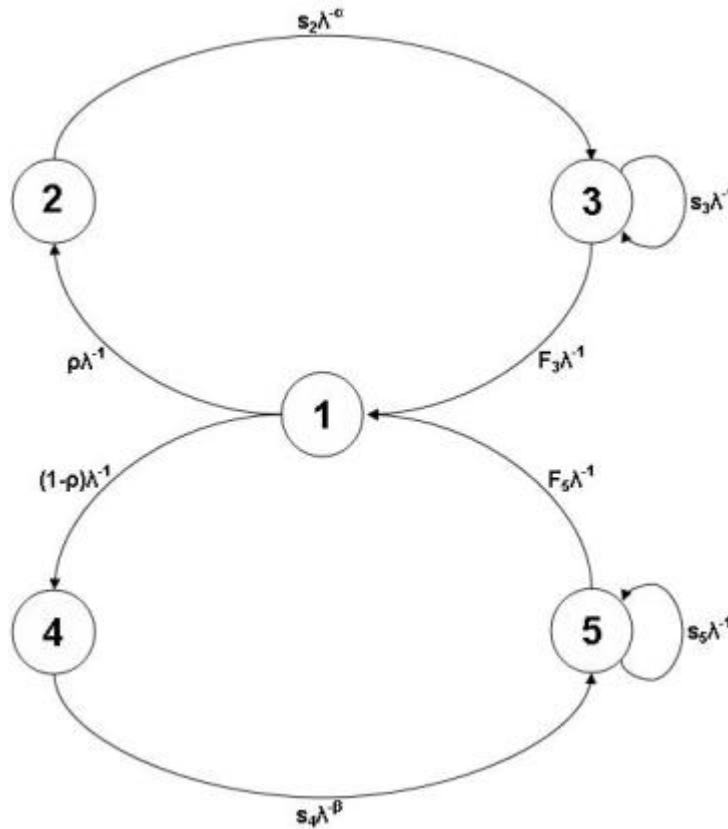


Figure 3.3: Two-sex z-transformed Life Cycle Graph

The exponents (alpha, beta) are there to indicate the number of projection intervals required to get from one stage to another. They can be used that way

to write down the characteristic equation, but not to project the population. For that you need an LCG and matrix that includes all the stages. The dynamics of this population can be described by a frequency dependent projection matrix (equation 3.5, for  $\alpha = 1$  and  $\beta = 1$ ) that corresponds to the LCG in figure 3.3, and the projection equation (equation 3.6) may be written in the standard fashion.

$$\mathbf{A}_{\mathbf{n}} = \left( \begin{array}{c|cc|cc} 0 & 0 & F_3 & 0 & F_5 \\ \hline \rho & 0 & 0 & 0 & 0 \\ 0 & s_2 & s_3 & 0 & 0 \\ \hline 1 - \rho & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & s_4 & s_5 \end{array} \right) \quad (3.5)$$

$$\mathbf{n}(t+1) = \mathbf{A}_{\mathbf{n}}\mathbf{n}(t) \quad (3.6)$$

The subscript  $\mathbf{n}$  on  $\mathbf{A}$  signifies that the projection matrix is dependent on values of  $\mathbf{n}$ , ie,  $\mathbf{A}$  is frequency dependent. In other words each element of  $\mathbf{A}$  is derived from a generalized mean of the entries in  $\mathbf{n}$ :

$$a_{ij} = \frac{k_{ij}M_{ij}\mathbf{n}}{n_j} \quad (3.7)$$

### 3.4 The Birth and Fertility Functions

The fertility functions  $F_i(\mathbf{n})$  summarize the demographic interactions between the sexes. The fertility function is most easily derived from the *birth function*  $B(\mathbf{n})$ .  $B(\mathbf{n})$  gives the number of births produced by the population  $\mathbf{n}$ . Letting  $n_m$  and  $n_f$  denote the number of males and females Caswell (2001) gives the following

functional forms for some  $B(\mathbf{n})$ , of which the harmonic mean birth function is generally regarded as the least flawed (Caswell, 2001):

$n_f$	(female dominant)
$n_m$	(male dominant)
$an_m + (1 - a)n_f$	(weighted mean)
$(n_m n_f)^{1/2}$	(geometric mean)
$\frac{2n_m n_f}{n_m + n_f}$	(harmonic mean)
$\min(n_m, n_f)$	(minimum)

The per capita fertility functions  $F_i(\mathbf{n})$  are related to the birth function in the following way:

$$F_i(\mathbf{n}) = \frac{B(\mathbf{n})}{2n_i} \quad (3.8)$$

For the harmonic mean birth function, where  $k$  is the clutch size, the female fertility function is:

$$F_f(\mathbf{n}) = \frac{kn_m}{n_m + n_f} \quad (3.9)$$

And the male fertility function is:

$$F_m(\mathbf{n}) = \frac{kn_f}{n_m + n_f} \quad (3.10)$$

Polygyny is easily incorporated in to the fertility function by introducing a parameter  $h$ , which represents a *harem* of average size. The harmonic mean birth function then becomes:

$$B(n_m, n_f) = \frac{2kn_m n_f}{(n_m + n_f h^{-1})} \quad (3.11)$$

$h > 1$  corresponds to polygyny,  $h = 1$  corresponds to monogamy, and  $h < 1$  to polyandry (where one female mates with multiple males). Figure 3.4 below shows the harmonic mean birth function (equation 3.11) as a function of the proportion of males and the harem size:

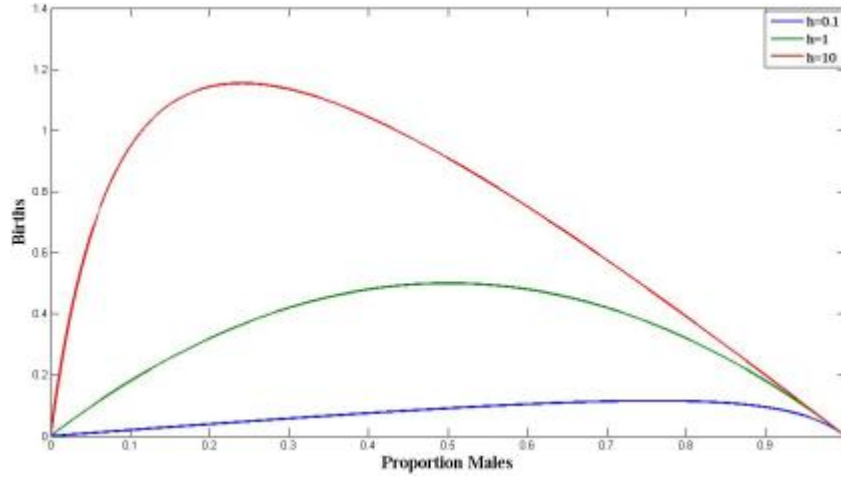


Figure 3.4: Harmonic Mean Birth Function for Males with Variable Harem Size

When  $h = 1$ , births are maximized when males and females are equally abundant. When  $h > 1$ , however, births are maximized when females exceed males. An analogous relationship may also be seen in the fertility (fecundity) functions below.

Thus, the harmonic mean fertility functions in equations 3.13 and 3.10 take the following form:

$$F_f(\mathbf{n}) = \frac{kn_m}{n_m + n_f h^{-1}} \quad (3.12)$$

$$F_m(\mathbf{n}) = \frac{kn_f}{n_m + n_f h^{-1}} \quad (3.13)$$

Figure 3.5 below shows the per capita male and female fecundities derived from the harmonic mean birth function with variable harem size:

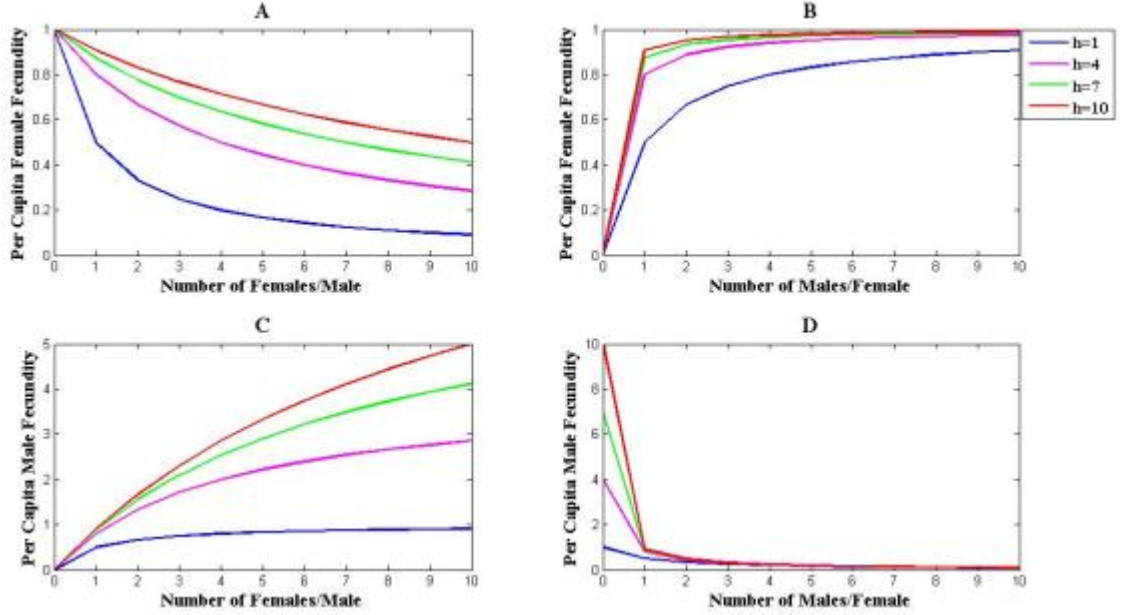


Figure 3.5: Harmonic Mean Per Capita Male and Female Fecundities with Variable Harem Size

### 3.5 Competition for Mates

An important factor, that is competition between age/stage classes for mates, was omitted from equation 3.7. According to equation 3.7,  $a_{ij}$  is negatively correlated with the abundance of only one stage ( $n_j$ ). Thus, the per capita production of stage  $i$  by stage  $j$  is reduced by competition *within* stage  $j$ , but **not** by competition with different stages. Human demographers have criticized birth functions that leave out competition, because the rate of marriage between males and females of given

ages depends not only on the relative abundance of those age groups, but on the abundance of other age groups as well (Caswell, 2001).

To incorporate mate competition in the fertility functions,  $F_i(\mathbf{n})$ , must include contributions of all possible combinations of male and female stages. Extending our two-sex LCG in figure 3.3 to incorporate two additional stage classes for each sex, a new LCG may be formed as in figure 3.6 below:

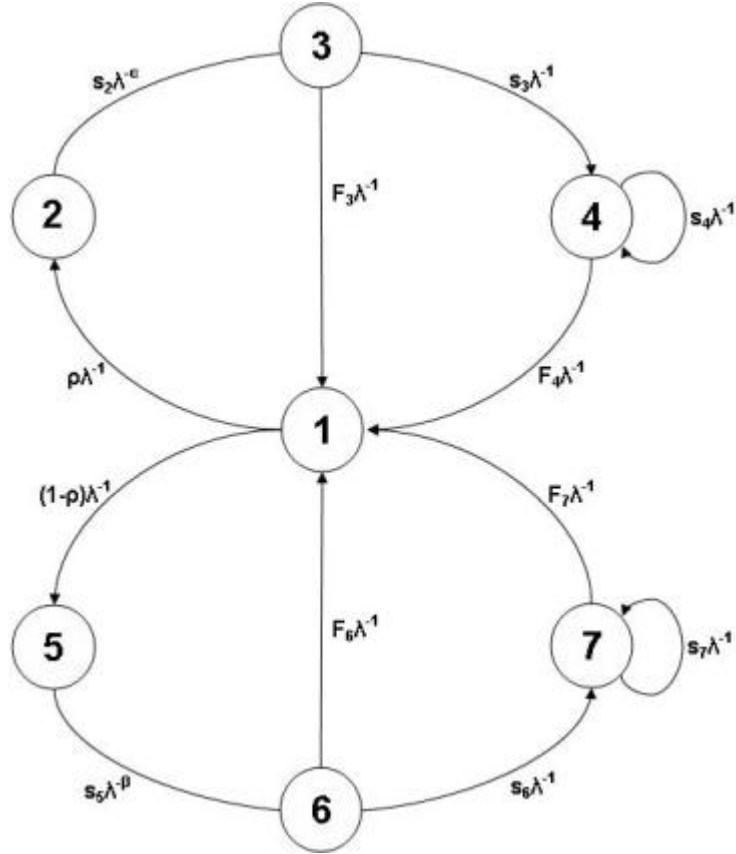


Figure 3.6: Two-Sex LCG with Competition Among Stages

Males represented by node 3 and node 4 then compete with each other for mating opportunities with node 6 and node 7 females. Similarly, node 6 and node 7 females compete with each other for mating opportunities with node 3 and node 4 males. The corresponding projection matrix (equation 3.14) is simply an extension

of equation 3.5:

$$\mathbf{A}_n = \left( \begin{array}{c|ccc|ccc} 0 & 0 & F_3 & F_4 & 0 & F_6 & F_7 \\ \hline \rho & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & s_2 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & s_3 & s_4 & 0 & 0 & 0 \\ \hline 1 - \rho & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & s_5 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & s_6 & s_7 \end{array} \right) \quad (3.14)$$

The fecundity terms in the top row are also modified to reflect competition, for example the fertility function for node 3 males then becomes:

$$F_3 = \frac{k_{36}M(n_3, n_6) + k_{37}M(n_3, n_7)}{n_3 + D(n_4)} \quad (3.15)$$

Here, k is the clutch size, M is the generalized mean (harmonic mean in this case) calculated as in equation 3.16

$$M(n_i, n_j) = \frac{2n_i n_j}{n_i + n_j} \quad (3.16)$$

and D is competition parameter that is zero for no competition, and may take on any value greater than zero to reflect increasing competition between stages.

### 3.6 Survival

As mentioned earlier entries on the diagonals signify probabilities of moving from one stage to the next. In biological terms, these are know as survivorship or simply



survival, and usually vary according to age and sex for any given species. There are many methods to calculate survival ranging from statistical methods applied to time-series and/or cross-sectional population data to direct estimation from life tables. Where data is unavailable, one may turn to published literature for survival estimates of the species under study or use survival estimates for related/similar species.

The main question in the context of population modeling and more so for harvesting species is whether the survival is density dependent (compensatory) or density independent (additive). Compensatory mortality (survival) is where hunting mortality is compensated for by a reduction in natural mortality (increase in survival), ie, it would remove the “doomed surplus” of individuals that would have succumbed to some other form of mortality such as disease, old age, or natural predation, resulting in a constant rate of survival despite removal of additional animals. Additive mortality, on the other hand, is exactly as implied by the name, adding to the natural mortality, thereby reducing survival proportionately the hunting or kill rate.

At high population densities, competition for limited resources such as food and shelter increases. Therefore, if the population is at or near its natural carrying capacity, survival is likely to be density dependent and independent if the population is below its natural carrying capacity (Cooch, 2007). This has important implications in the context of harvesting species, since a population below its natural carrying capacity is likely to display density independent survival and thus, be more vulnerable to harvest. As it approaches its carrying capacity however, some form of density dependence becomes more likely, and harvest may be compensatory,

### 3.7 Harvest

Harvest is easily incorporated in to either one-sex or two-sex matrix models by introducing a diagonal matrix having the same dimensions as the projection matrix. The projection equation may then be written as:

$$\mathbf{n}(t+1) = \mathbf{H}\mathbf{A}\mathbf{n}(t) \quad (3.17)$$

where  $\mathbf{H}$  is the harvest matrix. All ones on the diagonal mean no harvest, whereas numbers between zero and one signify harvest. If we wish to model the harvest of a specific age or sex class, we may keep all numbers as one, and change only that corresponding to the ages/sex class we want to harvest. In our simple two-sex example from section 3.3 then:

$$\mathbf{n}(t+1) = \left( \begin{array}{c|cc|cc} 1 & 0 & 0 & 0 & 0 \\ \hline 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0.8 & 0 & 0 \\ \hline 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 1 \end{array} \right) \left( \begin{array}{c|cc|cc} 0 & 0 & F_3 & 0 & F_5 \\ \hline \rho & 0 & 0 & 0 & 0 \\ 0 & s_2 & s_3 & 0 & 0 \\ \hline 1-\rho & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & s_4 & s_5 \end{array} \right) \left( \begin{array}{c} n_1 \\ n_2 \\ n_3 \\ n_4 \\ n_5 \end{array} \right) \quad (3.18)$$

The element  $H_{3,3} = 0.8$  signifies a harvest of 20 percent of node 3 males.

The discussion in the sections above provide us with all the elements needed to model two-sex population dynamics subject to harvest. The next chapter puts all these elements together to build and simulate a two-sex population projection model for a hunted ungulate, the Markhor (*Capra falconeri*), in Baluchistan, a western province of Pakistan.

CHAPTER 4  
CASE STUDY: TROPHY HUNTING OF MARKHOR IN  
PAKISTAN

## 4.1 Biology of Species

The Markhor (*Capra falconeri*) is a wild mountain goat and the national animal of Pakistan. The scientific classification of the Markhor is shown below in table 4.1:

Table 4.1: Scientific Classification of Markhor

Kingdom	Animalia
Phylum	Chordata
Subphylum	Vertebrata
Class	Mammalia
Order	Artiodactyla
Family	Bovidae
Subfamily	Caprinae
Genus	Capra
Species	<i>Capra falconeri</i>

Some literature (Cothran et al. (2005); Ellerman and Morrison-Scott (1951)) documents seven distinct subspecies of Markhor (based on horn shape and size), five of which are said to occur in Pakistan. Schaller and Khan (1975), however, disagrees with the classification based on horn shape and size alone and has reduced the sub-species occurring in Pakistan to two, ie, *Capra falconeri falconeri* and *Capra falconeri megaceros*. The two sub-species not only differ in the basic shape of their horns, ie, straight and flaring or divergent (see figure 4.1), but also in size and ruff length. To my knowledge, more recent and accurate genetic techniques however, have not been applied to wild Markhor populations to determine the exact number of subspecies.



Figure 4.1: The two *recognized* Sub-species of Markhor in Pakistan

“The common name, Markhor, is thought to have either originated from the Persian words ”mar” and ”khor”, loosely translated as ”snake-eater”, or from the Pushto words ”mar” and ”akhur”, translated as ”snake-horn”. Several linguistic camps favor the latter theory, as it seems to refer to the shape of markor horns. Since the species is entirely vegetarian, it would not make much sense to label it an eater of snakes” (Cothran et al., 2005).

#### 4.1.1 Geographic Range

Scattered populations of Markhor may be found throughout the arid and steppe regions of the western Himalayas. Countries of discontinuous distribution are limited to Afghanistan, India, Pakistan, Tajikistan, Turkmenistan, and Uzbekistan (Cothran et al., 2005). The species is adapted to mountainous terrain between 600 meters and 3600 meters elevation.

Population densities in Pakistan range from 1 to 9 individuals per square kilometer. The range of such herds is often extremely limited as a result of the moun-

tainous terrain which Markhors inhabit. A survey by (Schaller and Khan, 1975), in 1975 resulted in one of the more comprehensive data on the status and distribution of Markhor in Pakistan. See Figure 4.2:

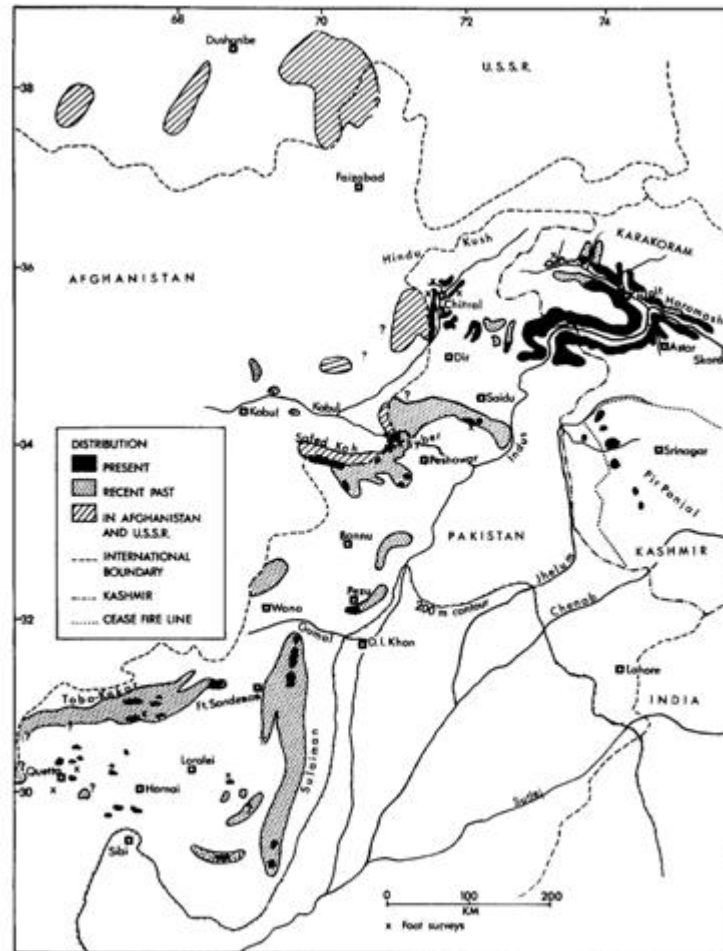


Figure 4.2: Distribution of Markhor, 1975

Since then besides individual unofficial surveys and accounts, the only detailed data on the distribution and status of the Markhor in Pakistan was carried out by the IUCN Caprinae Specialist Group in 1999 as part of a world wide survey on the status of wild sheep and goats and their relatives (Shackelton, Shackelton). They acknowledge that the distribution map shown in figure 4.2 is still relevant

today, but the population numbers are almost certain to be less than when Schaller carried out his study.

#### 4.1.2 Physical Description

*Capra falconeri* is highly sexually dimorphic in size. Males weigh between 80 and 110 kg, whereas females weigh only 32 to 50 kg. Body length varies between 140 and 180 cm, and the tail may add an additional 8 to 14 cm to the total length.

The relatively short coat of *C. falconeri* can range in color from light tan to dark brown, and even black. *Capra falconeri* differs from *Capra ibex* in that it lacks the extremely dense winter underwool possessed by the latter. Fringed beards are present in both sexes, but are thicker, longer, and more distinct in male markhorns (Cothran et al., 2005).

Light and dark color patterns, typical of all *C. falconeri* subspecies, are present on the lower legs. *Capra falconeri* lacks the knee tufts, inguinal and suborbital glands present in many species of goats inhabiting mountainous regions. Males and females both possess extremely bold, flared, corkscrew-like horns. These horns twist outward and may reach lengths up to 160 cm in males and 24 cm in females. The angle and direction of horn curvature varies among the subspecies of *C. falconeri*. Horn color varies from dark to reddish-brown (Cothran et al., 2005).

Although some might mistake *C. falconeri* for other members of the genus from a distance, the horns of markhorns make them quite unique in appearance. Northern populations of *C. falconeri* can be easily distinguished from *Capra aegagrus* by the dorsal crest and lower hanging beard in *C. falconeri*, as well as the differences in horn morphology and coloration (Cothran et al., 2005).

### 4.1.3 Reproduction

Markhors breed annually. Breeding occurs during fall and winter months. It is during this time that solitary males may temporarily join female herds. Number of offspring is 1 to 2 with an average of 1.5. The gestation period is 4.50 to 5.67 months with an average of 5.08 months. Time to weaning is 5 to 6 months (Cothran et al., 2005).

Female age at sexual or reproductive maturity 18 to 30 months, while male age at sexual or reproductive maturity is 36 months. Like most ungulates, *C. falconeri* is polygynous, where a single male mates with a *harem* of females. Markhors breed annually, with males competing aggressively during the rut for the right to sire the offspring of female herds (Cothran et al., 2005).

Markhors are usually born in the spring and summer months of May and June. The young are initially born in a shallow earthen hollow. They are able to walk soon after birth, and can travel with the mother. Mothers provide nourishment (milk) and protection to their growing young. They stay with the mother for approximately 6 months, although there are several reports of kids remaining with the mother thereafter. Males are not reported to participate in parental care (Cothran et al., 2005).

### 4.1.4 Lifespan/Longevity

The lifespan of *C. falconeri* ranges from 11 to 13 years. The species is both hardy and resilient, and as a result, small herds may be successfully reared and maintained in captivity (Cothran et al., 2005).

### **4.1.5 Conservation Status**

*C. falconeri* is prized among trophy hunters and members of the Asian medicine market. They face habitat competition from both domestic livestock and local agriculture. As a result, all populations of feral *C. falconeri* have been steadily declining over the past 40 years. *C. falconeri* was classified as endangered and conservation-dependant in 1996 by the IUCN, indicating that the long-term survival of this species is heavily dependent on the initiation and maintenance of conservation programs (Cothran et al., 2005).

## **4.2 Calibration of Biological Model**

*C. falconeri* displays both sexual dimorphism and polygyny, (see subsections 4.1.2 and 4.1.3). Since the Markhor's life span is about 13 years (see subsection 4.1.4 and males older than 6 years are hunted (2.1), I defined a 6-stage-classified model for both sexes combined, ie, one year olds, two years olds, three year olds, four year olds, five year olds, and six year olds and greater based on the maximum age of Markhor reported 4.1.4..



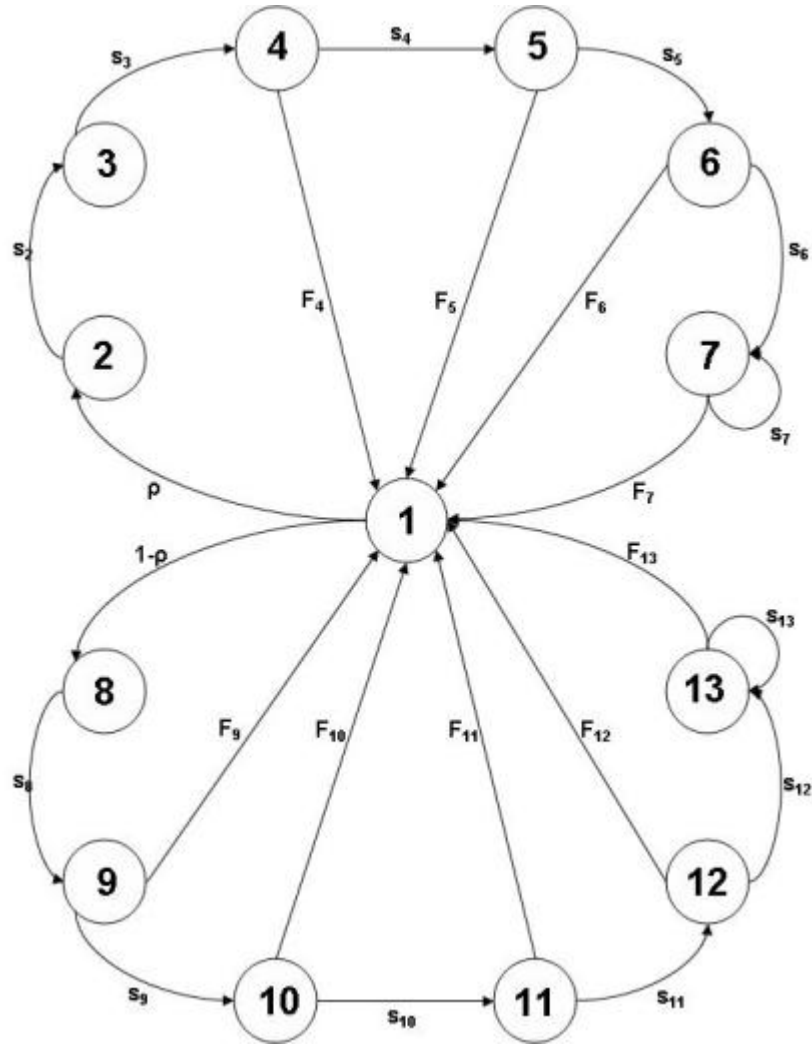


Figure 4.3: Two Sex Life Cycle Graph

Node 1 represents unborn zygotes whose sex is yet to be determined. Then, nodes 2 through 7 represent males and 8 through 13 represent females. A self loop on nodes 7 and 13 means that it represents more than one age class such that those 6 years old and greater remain in that stage until death. Here, the resultant  $13 \times 13$  matrix contains the male and female sex ratio in the first column where  $\rho$  is the male sex ratio. The top row contains male fecundity in the left and female fecundity in the right. Male survival is then given in the upper left

quadrant following the first row and first column, and female survival is given in the lower right quadrant. All other entries are zeros.

The modeling approach was to begin with a deterministic, density-independent Leslie matrix population model that describes the average demography of the Markhor population. The matrix entries themselves were derived assuming a birth-pulse, pre-breeding design. I then examined progressively more complex modeling scenarios that incorporated regulatory effects as well as a revenue generating linear demand curve for hunting licenses.

Thus, following from equation 3.6, the population may be projected according to:

$$\mathbf{n}(t+1) = \begin{pmatrix} 0 & 0 & F_3 & F_4 & F_5 & F_6 & F_7 & 0 & F_9 & F_{10} & F_{11} & F_{12} & F_{13} \\ \rho & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & s_2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & s_3 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & s_4 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & s_5 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & s_6 & s_7 & 0 & 0 & 0 & 0 & 0 & 0 \\ \hline 1-\rho & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & s_8 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & s_9 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & s_{10} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & s_{11} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & s_{12} & s_{13} \end{pmatrix} \begin{pmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \\ n_5 \\ n_6 \\ n_7 \\ \hline n_8 \\ n_9 \\ n_{10} \\ n_{11} \\ n_{12} \\ n_{13} \end{pmatrix} \quad (4.1)$$

### 4.2.1 Parametrization

Direct measures of survival and fecundities for the Markhor are unavailable. However, they may be approximated by assuming similarities between other mountain goats. One such study that measures age and sex specific survival in five ungulate species was carried out by Loison et al. (1999). Furthermore, Festa-Bianchet et al. (2003) found that density dependence is unlikely in adult male ungulates, but survival is more likely a function of age. They do admit however, that males of dimorphic and polygynous species may show density dependence, and that increasing density may lower overall adult survival in naturally regulated populations but not in heavily harvested populations where few animals reach senescence. Additionally, for juveniles, mortality increases at high density (Festa-Bianchet et al., 2003). Alejandro Gonzalez Voyer (2003) state that hunting mortality appears to be additive in native populations of ungulates.

Another study of alpine ibex (Jacobson et al., 2004) however, found weak density dependence in the ibex population, and the Festa-Bianchet et al. (2003) and Alejandro Gonzalez Voyer (2003) studies did not look at populations at or above carrying capacity. Clutton-Brock et al. (1997) studied stability and instability in Soay sheep and Red deer populations, and found that increases in population density depress both survival and fecundity. The Clutton-Brock et al. (1997) study used survival functions decreasing in total population for the Soay sheep and Red deer, and parameterized them using maximum likelihood techniques on detailed population data collected over twenty years for both species. Unfortunately, such data is not available for the Markhor in Pakistan, therefore a functional form of density dependence can not be parameterized in a similar fashion.

I therefore assume a very simple functional form of density dependence-a basic

threshold model, which is homogenous below the threshold point (ie, survival rates vary by age but are independent of density up to the threshold point), and is decreasing in total population above the threshold, and takes the following form (to approximate one of the representative shapes of density dependent functions as given in McCullough (1999)):

$$\mathbf{s}_{it} = \overline{s}_i - \frac{N_t}{10000^{1.15}} \quad (4.2)$$

Here,  $\mathbf{s}_{it}$  is the survival rate of age class  $i$  at time  $t$ ,  $\overline{s}_i$  is the survival rate of age class  $i$  below the threshold,  $N_t$  is the total population at time  $t$ , and the carrying capacity is assumed to be 10000 animals. I varied the exponent on carrying capacity until the simulated population matched the six years of, admittedly not very good, data ((see Frisina, 2000)) on the Markhor population under consideration as closely as possible. Validity of such a threshold model may be established by other studies on ungulate population dynamics, most notably by Clutton-Brock et al. (1997), which found that survival for a Soay sheep population falls sharply above a threshold.

The Loison et al. (1999) study found the survival of prime age adults to vary between 0.85-0.95, with evidence of senescence, ie, decrease in survival for old aged members of the population. They also found female survival to be higher than male survival. Estimates of survival for juveniles was assumed to be less than the minimum survival of prime age adults given, and also more sensitive to high population density as suggested by Festa-Bianchet et al. (2003). The survival rates,  $(\overline{s})$ , below the threshold were therefore taken in the range provided by the Loison et al. (1999) study.

The fecundities were estimated using the harmonic mean birth function, incorporating interstage mate competition and polygyny (see Appendix A for formulas used to calculate fecundities). Though fecundities are frequency dependent, in ungulates they are known to decrease with increasing population density (Clutton-Brock et al., 1997). This was incorporated by increasing the values for the competition parameters in the fecundity function for population levels above the assumed carrying capacity. Both symmetric and asymmetric competition was simulated.

Harem size ( $h_i$ ) was varied according to the age class, assuming larger harems for older age classes.

The clutch size ( $k_{i,j}$ ) was taken to be 1 for node 8 (2 year old females) and 1.5 for all other (3 year and older) female nodes (see subsection 4.1.3).

The value for  $\rho$  was estimated from the data on one specific Markhor population in the Torgar area of Pakistan (Frisina, 2000) and taken to be equal to 0.44.

## 4.2.2 Biological Model Simulation, and Analysis

The initial population vector  $\mathbf{n}(t)$ , was taken from the data given in Frisina (2000). The population was first projected without density dependent survival, competition for mates, or harvest, for 100 years (figure 4.4).

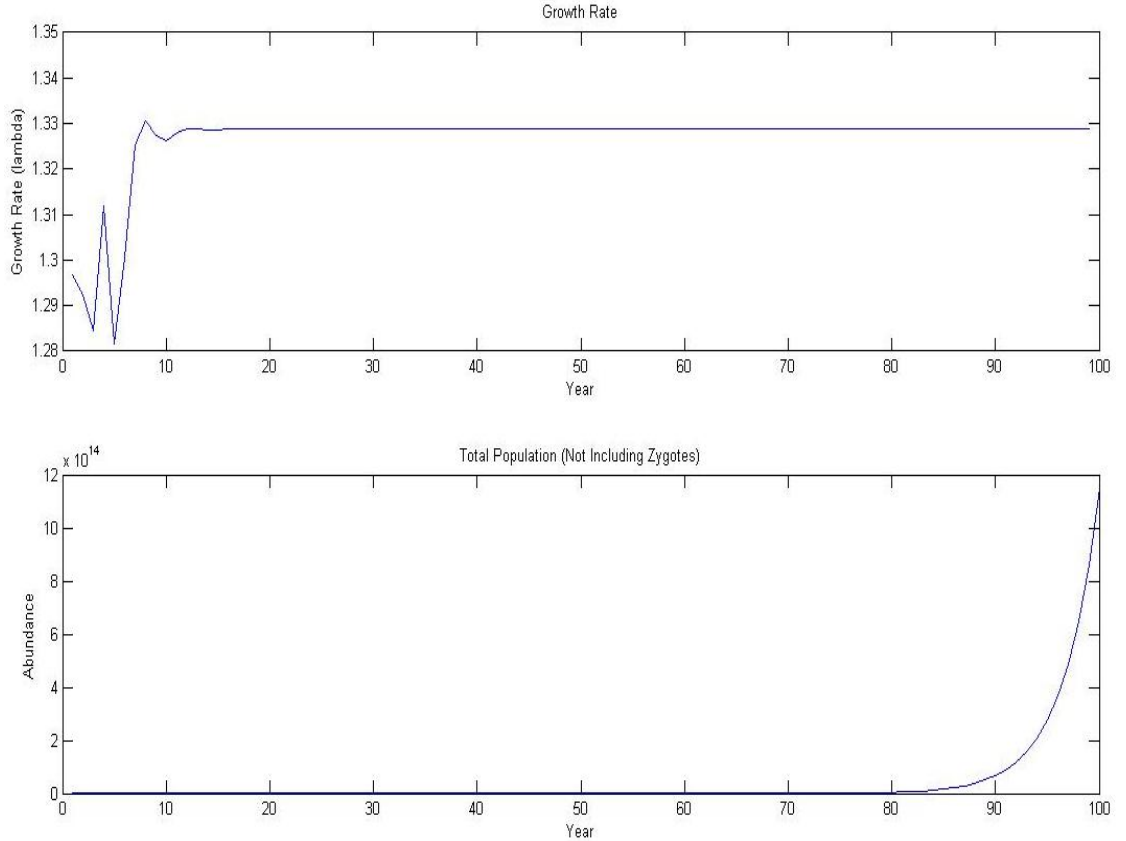


Figure 4.4: Dynamics for Density-Independent Survival and No Competition for Mates

The total population displays the classical exponential rise and the projected growth rate converges, after initial oscillations, to a constant value. While the total population numbers shown in figure 4.4 are not very realistic, the important thing to note here is the convergence of the projected growth rate. Population growth is unimpeded for the entire time growth is considered. Left unchecked it would continue to grow exponentially whenever  $\lambda > 1$ . Thus, exponential population growth is considered density-independent because abundance does not affect the rate of population growth. In other words the population converges to a stable age distribution (SAD), where all age classes eventually grow at the same rate (see figure 4.5).

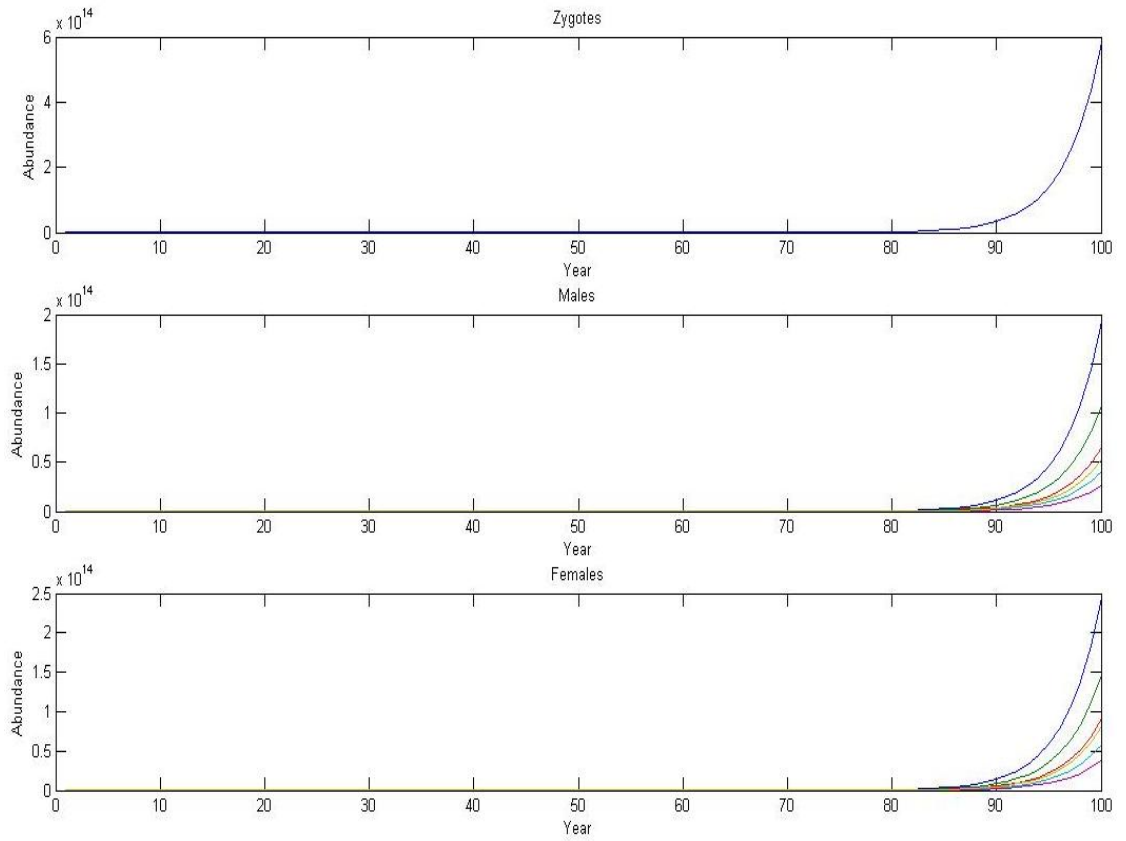


Figure 4.5: SAD for Density-Independent Survival and No Competition for Mates

Because populations can not grow exponentially forever, as a result of resource limitations and other conditions of the environment, the basic exponential growth model needs to be modified. As already mentioned in the section on parametrization above, the vital rates will display some form of density dependence. The following figures show simulation results for various combinations of density-dependent survival and symmetric and asymmetric competition for mates. Although symmetric competition is unlikely in the real world, it was simulated to contrast it with, and gain a better understanding of how, asymmetric competition affects population dynamics.

Thus, the population was then simulated with density dependence but without

competition for mates or harvest (figure 4.6).

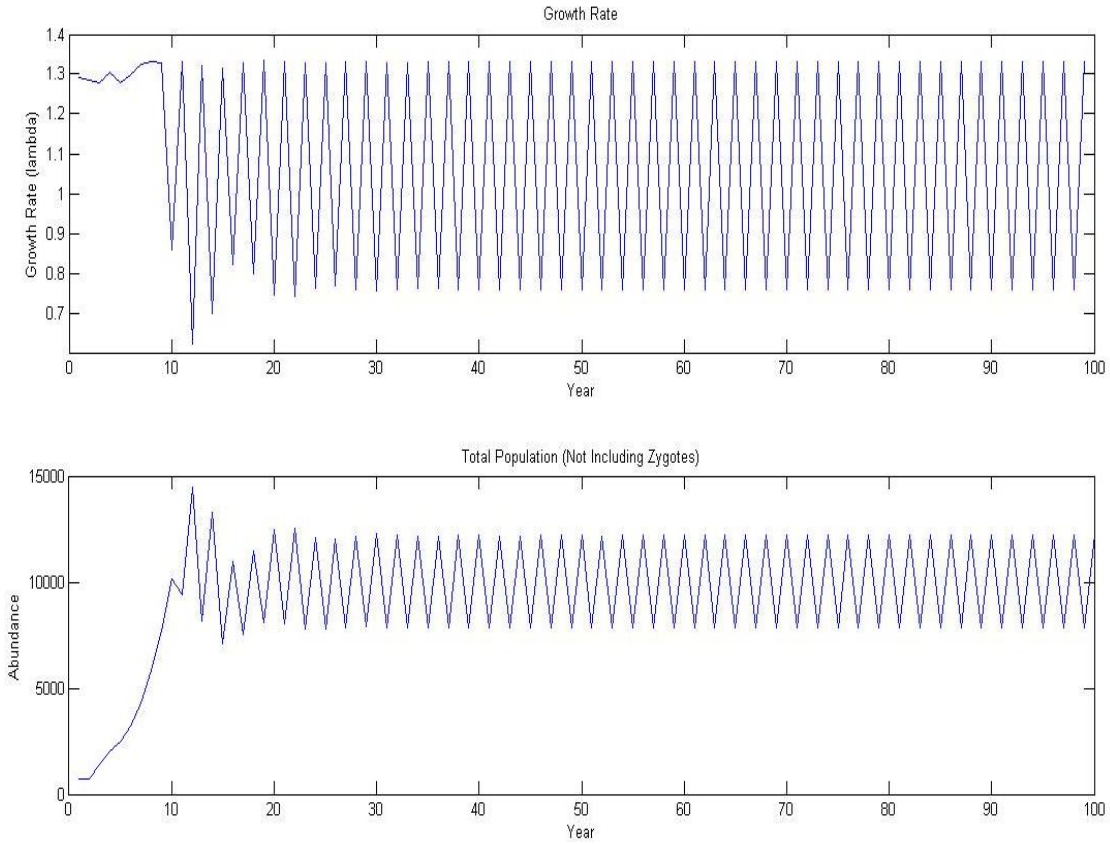


Figure 4.6: Dynamics for Density-Dependent Survival and No Competition for Mates

The drastic change in dynamics because of density-dependence is obvious. In fact the population now displays chaotic behavior both in terms of the growth rate and consequently its abundance. Chaos may be found in almost every kind of nonlinear ecological model (Caswell, 2001), and the dynamics shown in figure 4.6 show a 2-cycle convergence. The introduction of stage structure in the form of age classes has been shown to induce population cycles in both discrete-time matrix models and continuous time models (de Roos and Persson, 2003). Essentially, these cycles come about through negative feedback mechanisms, in particular density



dependence that acts on fecundity or survival probabilities (de Roos and Persson, 2003).

The population was then simulated with symmetric competition for mates but without density dependence or harvest (figure 4.7).

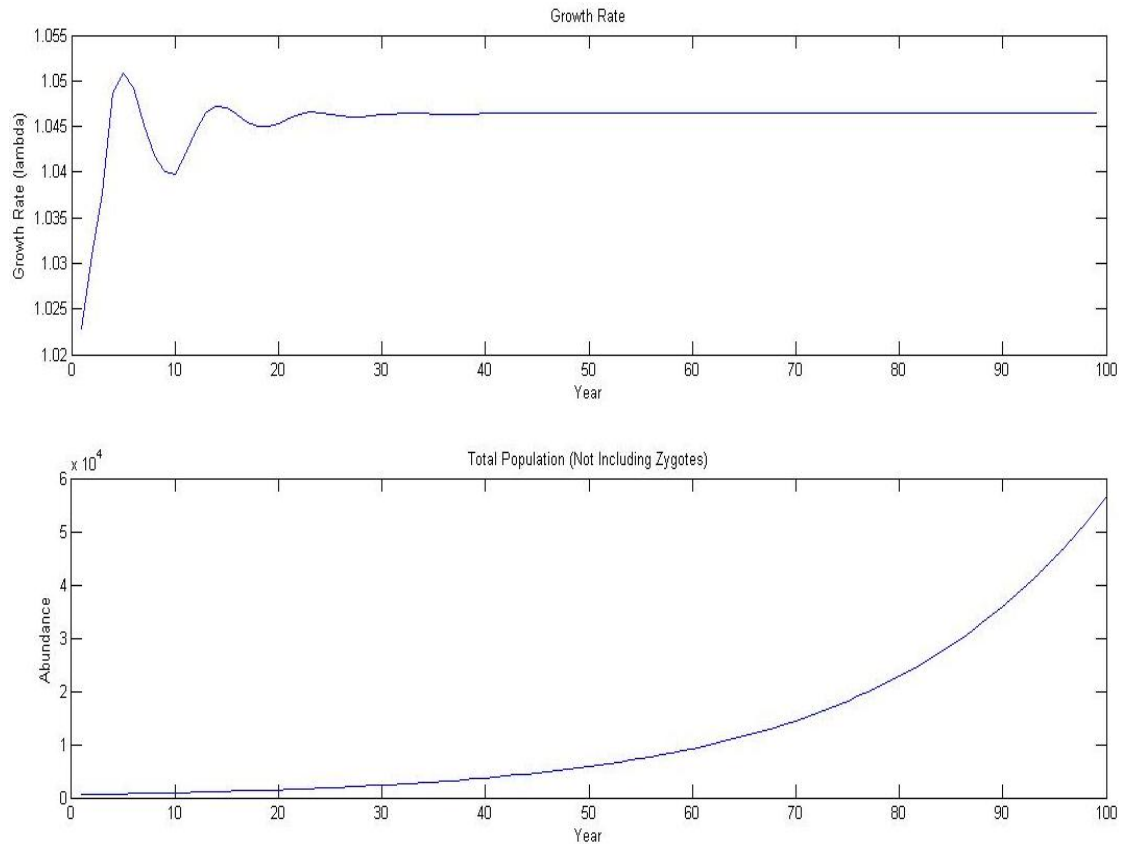


Figure 4.7: Dynamics for Symmetric Competition for Mates and Density-Independent Survival

Dynamics for symmetric competition and no density-dependence are almost exactly like those for no competition and no density-dependence, ie, exponential growth and achievement of an SAD. The main difference between the two is a slightly lower projected growth rate and less “severe” exponential rise for the symmetric competition model. Increased competition (whether symmetric or asym-

metric) is expected to lower projected growth, therefore the dynamics in 4.7 are unsurprising.

When symmetric competition for mates and density dependence is combined however, we again obtain cyclic dynamics as shown in figure 4.8 below:

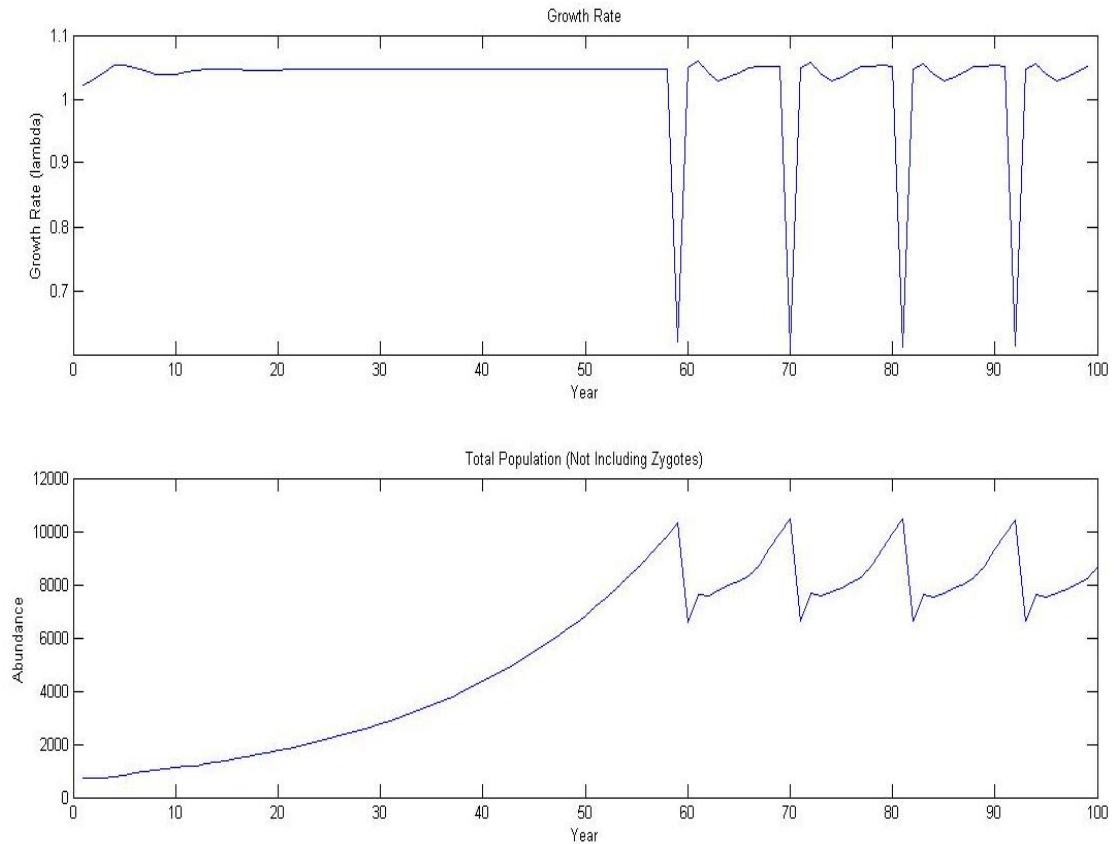


Figure 4.8: Dynamics for Symmetric Competition for Mates and Density-Dependent Survival

It is obvious from the figure that the cyclic dynamics are a result of density dependence as found in the earlier simulation (see 4.6). It takes slightly longer in this simulation for the dynamics to start cycling however, obviously because the density dependence does not kick in until the population has reached the carrying capacity. That is, the projected growth rate and total population show similar

dynamics as our model with symmetric competition until the about the sixtieth year, when it reaches the specified threshold population of ten thousand animals.

The population was then simulated with asymmetric competition for mates but without density dependence or harvest (figure 4.9).

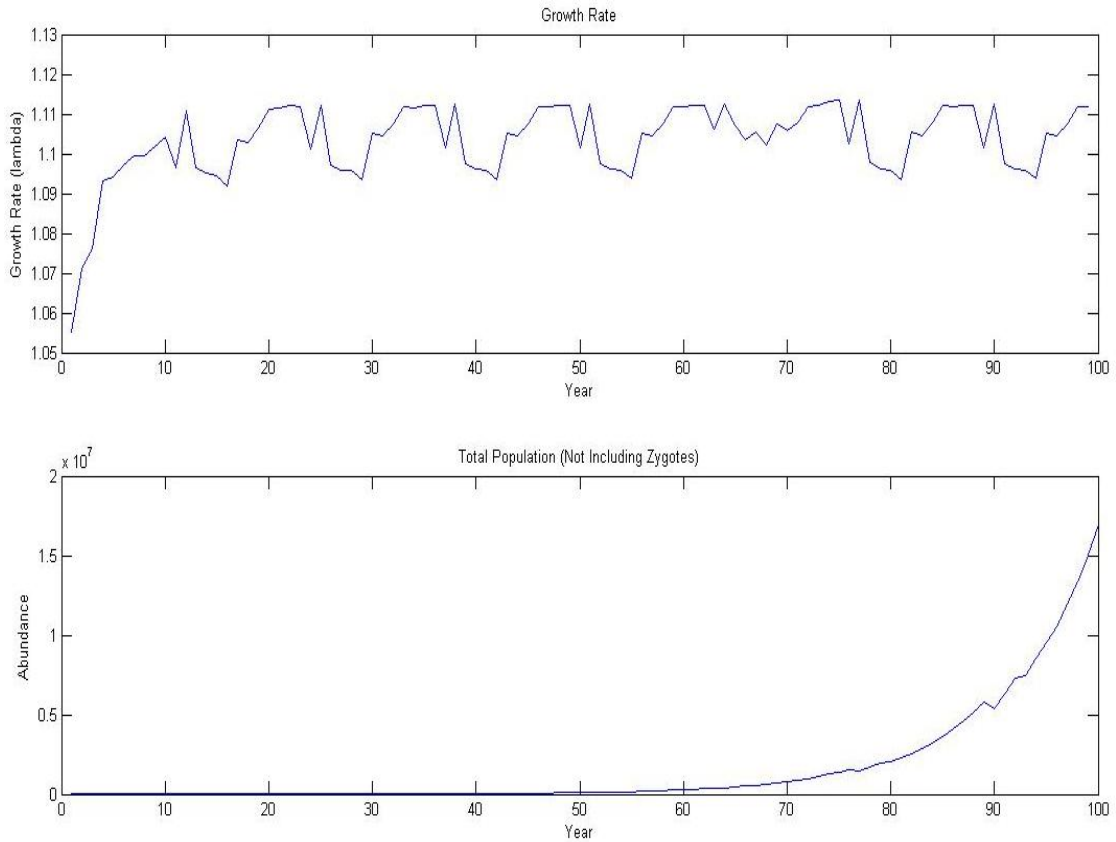


Figure 4.9: Dynamics for Asymmetric Competition for Mates and Density-Independent Survival

Asymmetric competition was simulated by making older age classes more competitive in mating than younger ones. The dynamics as seen in figure 4.9 are relatively stable with respect to the total population. And though the the growth rate appears to be highly variable, it remains above one, and within a very narrow range. The abundance therefore shows an exponential-like rise, with occasional

dips associated with falls in the growth rate.

Finally, the population was simulated with both asymmetric competition for mates and density dependence (4.10). Thus, for reasons already discussed, this particular model was assumed to be the one most closely describing the “real” population dynamics of the Markhor.

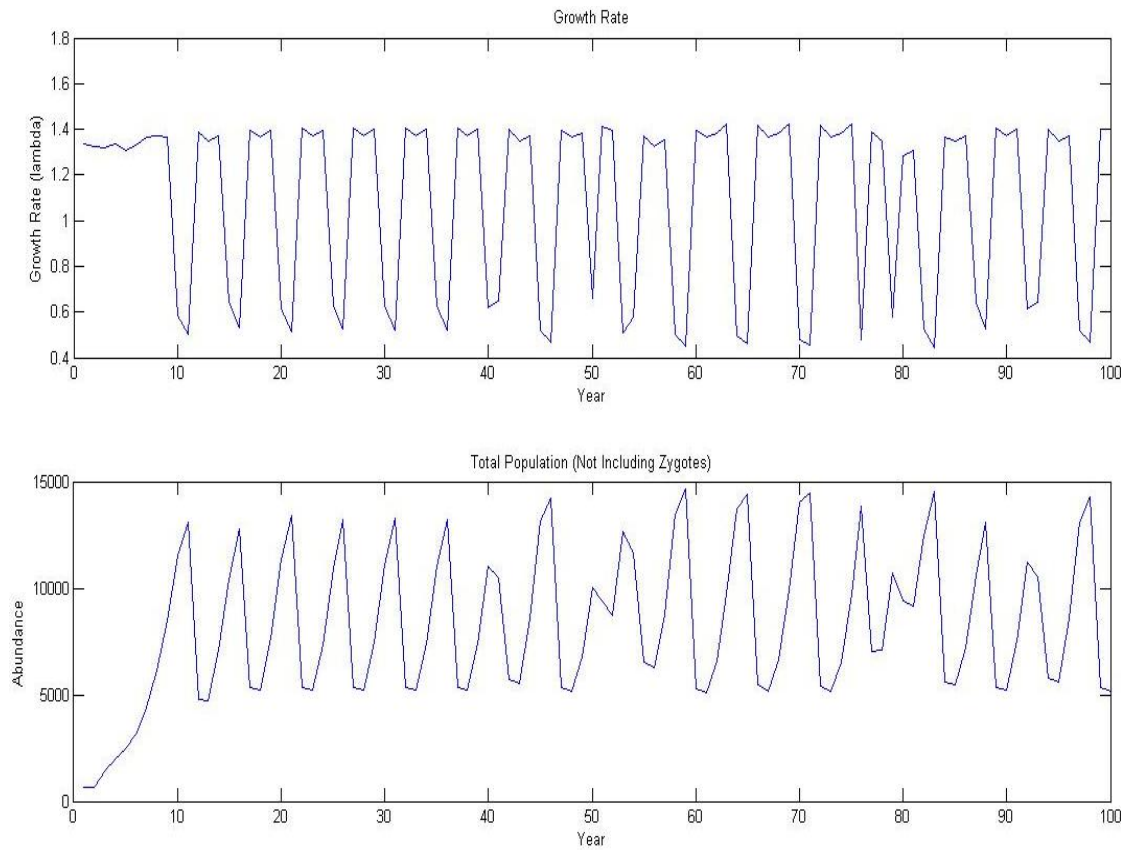


Figure 4.10: Dynamics for Asymmetric Competition for Mates and Density-Dependent Survival

While many populations of large mammals show considerable stability, studies of several ungulate populations provide evidence of oscillations that vary widely in regularity and periodicity. Periods of rapid decline followed by recovery have also been documented in populations of wild sheep, temperate deer, and tropical

antelope, while persistent instability occurs in several populations of feral sheep and goats (Clutton-Brock et al., 1997).

Fluctuations in the size of our simulated population are likely a consequence of density-dependent mortality. Survival falls sharply above a threshold, and different age classes are affected disproportionately. When population numbers exceed the carrying capacity and survival is low, recruitment is depressed. To see how we might stabilize the simulated population, I changed the fecundity and survival rates in the final model (figure 4.10) to see what affect this would have on the dynamics. Reducing fecundity and the affect of density-dependence on survival either individually or simultaneously had the affect of stabilizing the population. Reducing fecundity had a more stabilizing affect than reducing density-dependence (see figures 4.11 and 4.12 below).

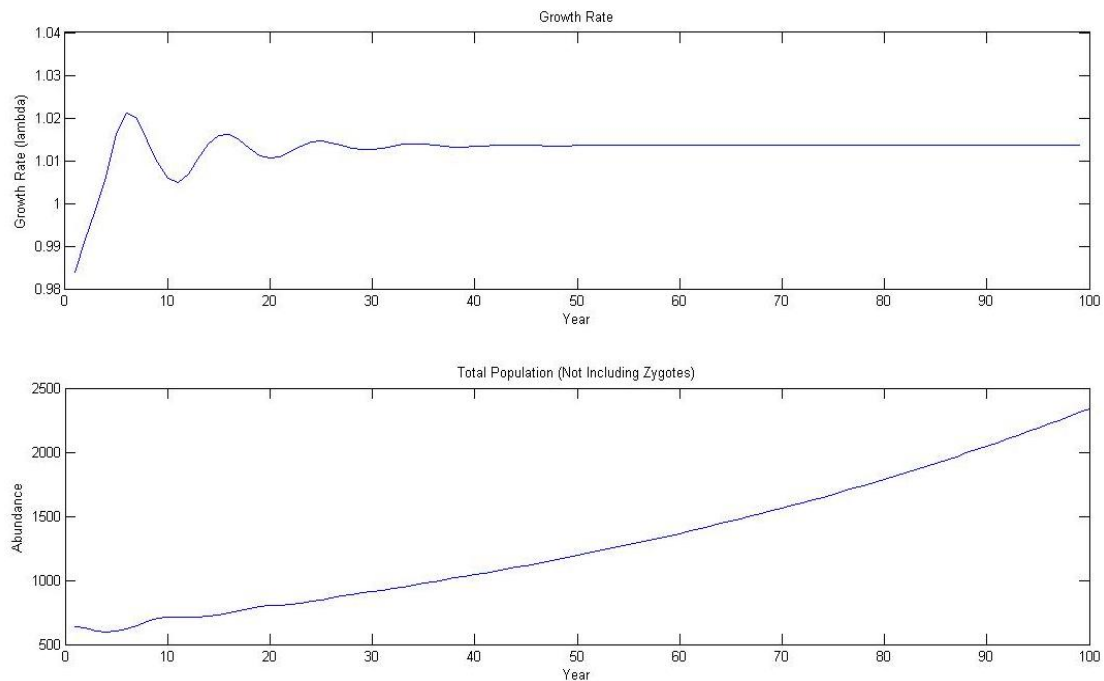


Figure 4.11: Reduced Fecundity

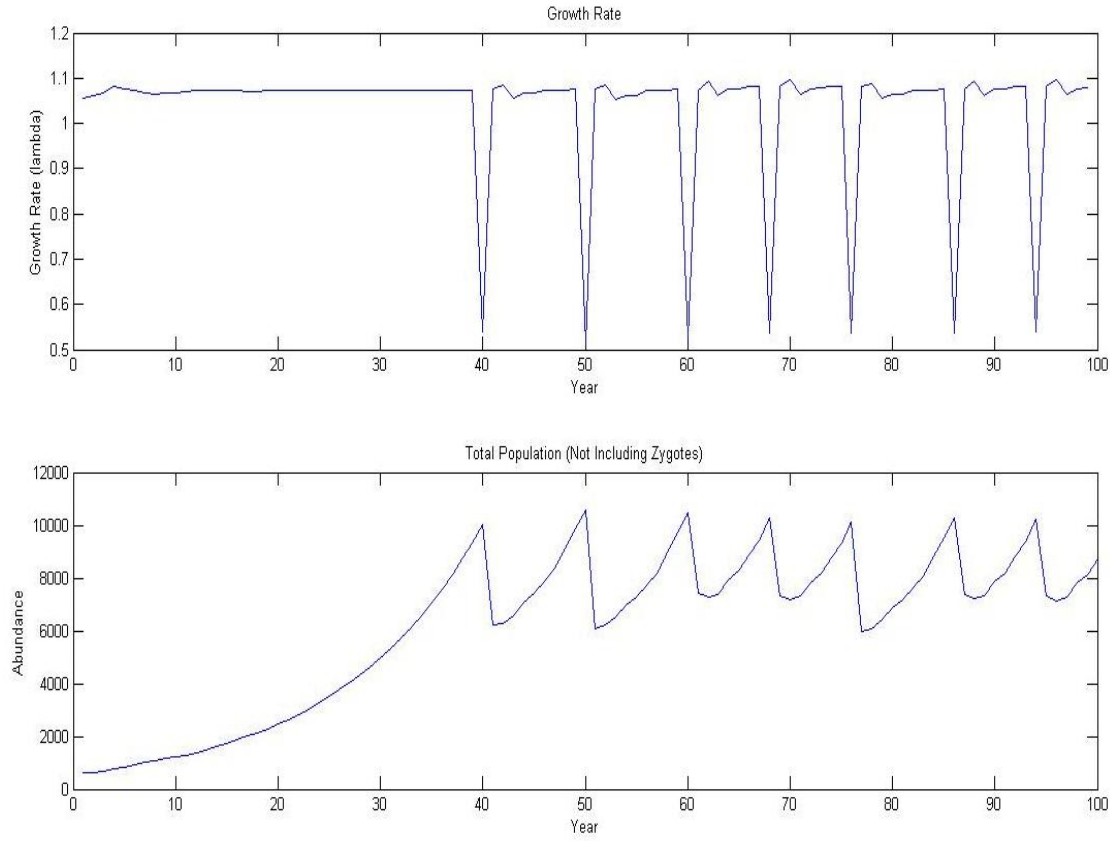


Figure 4.12: Reduced Density Dependence

This is in line with our earlier simulations without density dependence and symmetric competition. Therefore, we can conclude that the cyclic behavior is caused by the negative feedback mechanisms, in particular density dependence that acts on fecundity or survival probabilities and cross-cohort competition, as suggested by de Roos and Persson (2003), Nisbet and Onyiah (1994), and Clutton-Brock et al. (1997).

## Harvest

The current quota for hunting, set by authorities, for the Markhor population under consideration, is five males six years old or greater. This translates to less than one percent of the total estimated population of close to two thousand animals, and is approximately two percent of the six years old or greater male population.

Harvest may be simulated either as a proportion (percentage) of the population using the harvest matrix described in the previous chapter, or as a constant. I simulated trophy harvest for existing quota using both methods and the results are shown in figures 4.13 and 4.14 below.

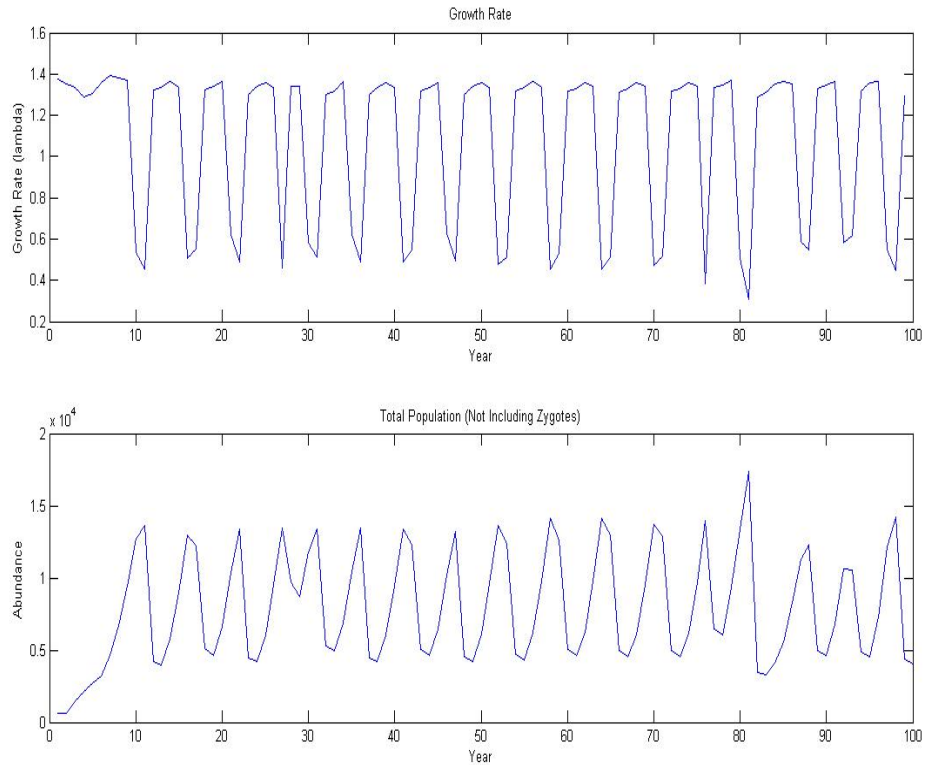


Figure 4.13: Growth Rate and Total Population - Two Percent Harvest

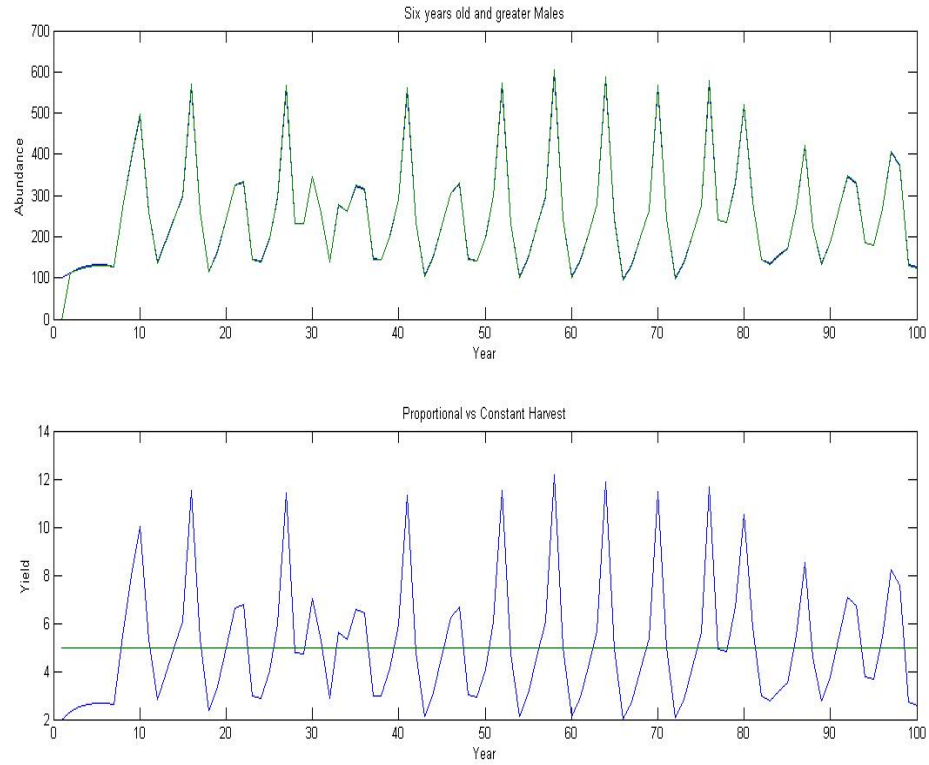


Figure 4.14: Males  $\geq 6$  years old - Proportional and Constant Harvest

In the density-dependent model with asymmetric competition for mates, neither proportionate nor constant harvest had any effect on “pattern” of projected growth dynamics even for harvest rates as high as ninety percent of the targeted age class. In fact, figures 4.10 and 4.13 are identical. Increasing the harvest rate had no effect on the population dynamics, suggesting that dynamics are more dependent on other age classes and/or are perhaps female dominant. This also suggests, that the current quota of five animals per year is sustainable.

The following figures show results for alternative harvesting strategies, such as both-sex and multiple age-class harvest.



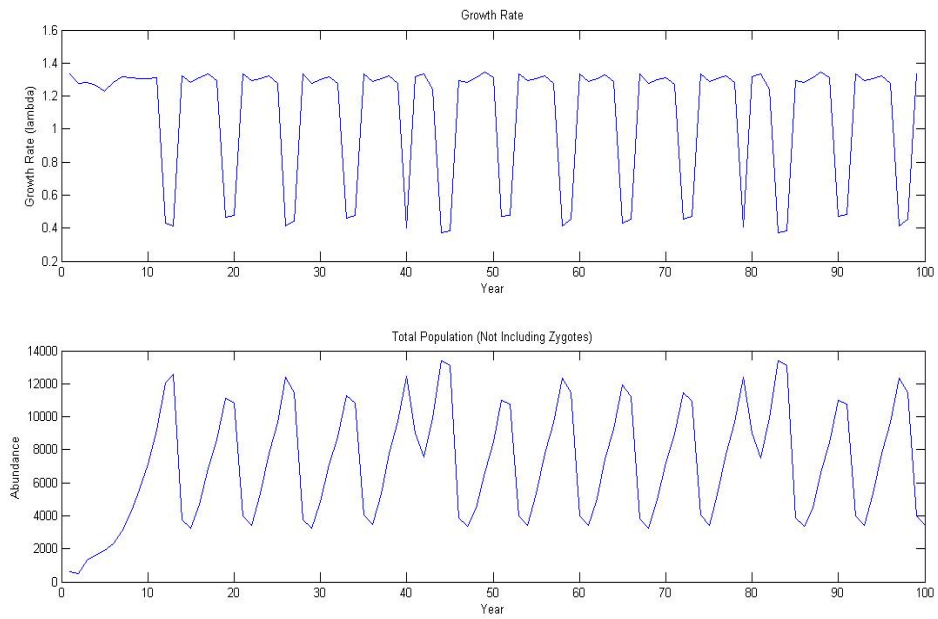


Figure 4.15: Females  $\geq 6$  years old only Harvest

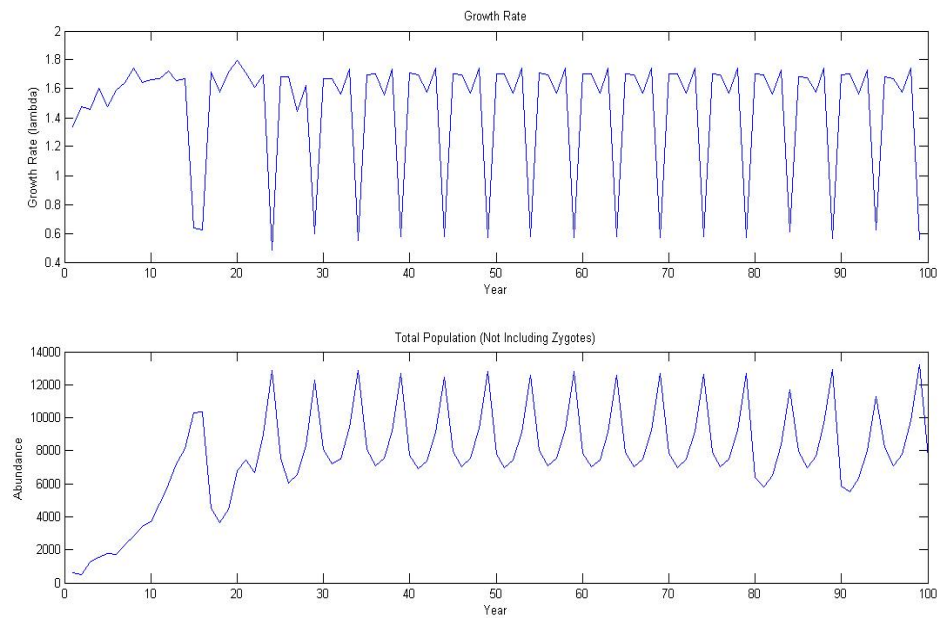


Figure 4.16: Multiple Male Age Class Harvest

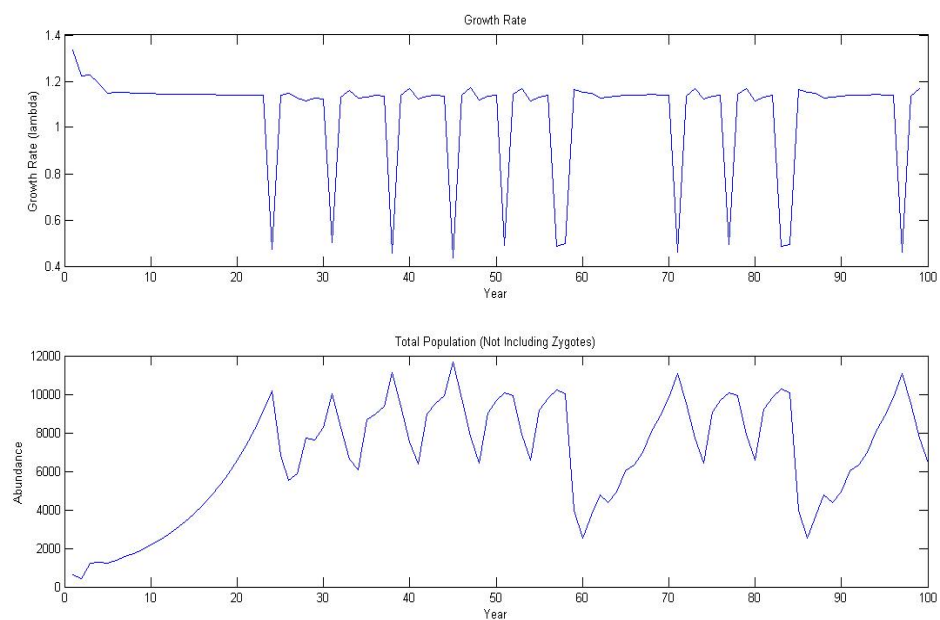


Figure 4.17: Multiple Female Age Class Harvest

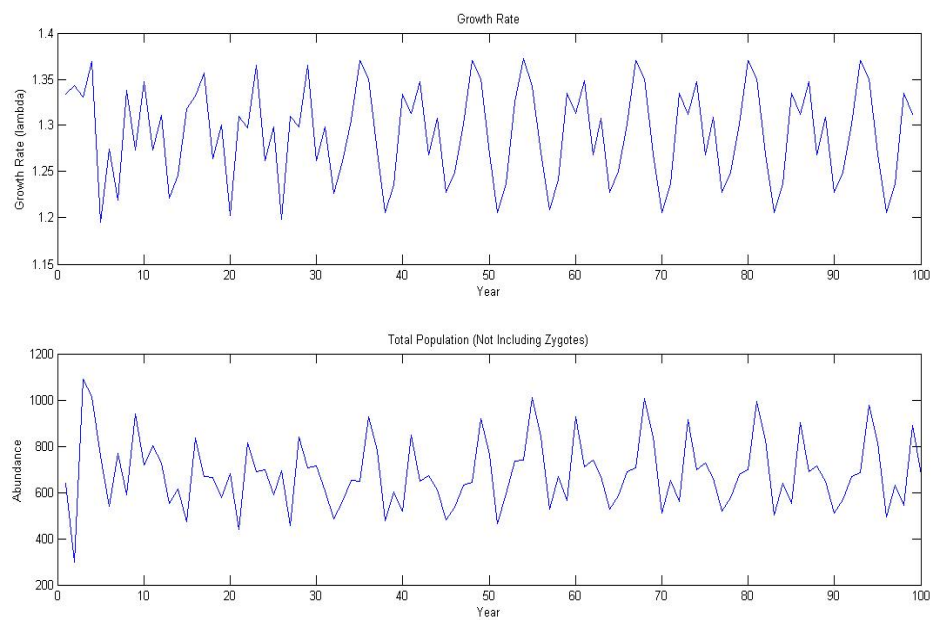


Figure 4.18: Both Sex Multiple Age Class Harvest

Of note are figures 4.16, 4.17, and 4.18, in that population dynamics are altered in terms of cyclicity in projected growth rate and total abundance. For same-sex multiple age-class harvest the amplitude of the growth rate remains unchanged from the no-harvest strategy, but the periodicity increases for males and decreases when females are targeted.

When multiple age-classes of both sexes are harvested, the dynamics appear to become more random and chaotic, though of note is the amplitude of the projected growth rate, which decreases in contrast to the no-harvest strategy. The total population however, persists significantly below the carrying capacity, as compared to the other harvest strategies.

## CHAPTER 5

### ECONOMIC ASPECTS

The purpose of this chapter is to assess, by means of a literature review of auction theory and monopoly pricing, whether the existing delivery mechanism is optimal for the sale of permits, or whether there is an alternative mechanism(s) that might be better. An optimal mechanism is defined as one which maximizes the seller's expected revenues.

#### 5.1 Auction Theory

Four basic types of auctions are widely used and analyzed:

1. In the *ascending auction*, the price is successively raised until only one bidder remains, and that bidder wins the object at the final price. This auction can be run by having the seller announce prices, or by having the bidders call out prices themselves, or by having bids submitted electronically with the best current bid posted.
2. The *descending auction* works in exactly the opposite way: the auctioneer starts at a very high price, and then lowers the price continuously. The first bidder who calls out that she accept the current price wins the object at that price.
3. In the *first-price sealed-bid auction* each bidder independently submits a single bid, without seeing others' bids, and the object is sold to the bidder who makes the highest bid. The winner pays her bid, ie, the price is the highest or "first" price bid.

4. In the *second-price sealed-bid auction* (also called a Vickrey auction), also, each bidder independently submits a single bid, without seeing others' bids, and the object is sold to the bidder who makes the highest bid. However, the price she pays is the second-highest bidder's bid, or "second" price.

Furthermore, there are two basic models of auctions: the private-value model, in which each bidder knows how much she values the object(s) for sale, but her value is private information to herself; in the pure common-value model, by contrast, the actual value is the same for everyone, but bidders have different private information about what that value actually is. With private values, in the ascending auction, the dominant strategy is to stay in the bidding until the price reaches your value, that is, until you are just indifferent between winning and not winning. The next-to-last person will drop out when her value is reached, so the person with the highest value will win at a price equal to the value of the second-highest bidder. Furthermore, Klemperer (2004) states that a second-price sealed-bid private-values auction is analogous to the ascending auction in that the person with the highest value will win at a price equal to the value of the second-highest. Here however, "truth telling" is a dominant strategy, that is it is optimal for a player to bid her true value, whatever other players do (Klemperer, 2004).

A key result in auction theory is the Revenue Equivalence Theorem (RET): *Assume each of a given number of risk-neutral buyers of an object has a privately known signal independently drawn from a common, strictly increasing, atomless distribution. Then any auction mechanism in which (i) the object always goes to the buyer with the highest signal, and (ii) any bidder with the lowest-feasible signal expects zero surplus, yields the same expected revenue (and results in each bidder making the same expected payment as a function of her signal).* Thus, the RET

tells us that the seller can expect equal profits on average from all standard (and many non-standard) types of auctions, and that buyers are also indifferent among them all.

Much of auction theory can be understood in the terms of this theorem, and how its results are affected by relaxing its assumptions of: (i) a fixed number; (ii) of symmetric; (iii) risk-neutral bidders; (iv) who each want a single unit; (v) have independent information; (vi) and bid independently (Klemperer, 2004). Myerson (1981) shows how to derive optimal auctions (ie, auctions that maximize the seller's expected revenue) when the assumption of symmetry fails. Maskin and Riley (1984) consider the case of risk-averse bidders, in which case the first-price sealed-bid auction is the most profitable of the standard auctions. Milgrom and Weber (1982) analyzed auctions when the assumption of independent information is replaced by one of affiliated information (ie, if one bidder has more optimistic information about the value of the prize, it is likely that other bidders' information will also be optimistic), and showed that the most profitable standard auction is then the ascending auction.

“For practical auction design, it is probably most important to remove the assumptions that the number of bidders is unaffected by the auction design, and that the bidders necessarily bid independently of each other; the sealed-bid designs frequently (but not always) both attract a larger number of bidders and are better at discouraging collusion than are ascending designs” (Klemperer, 2004). For practical auctions design Klemperer (2004) suggests that a good auction needs to be tailored to the specific details of the situation, and that encouraging entry and discouraging collusion are the most critical issues to consider (Klemperer, 2004).

There is also a close analogy between the theory of optimal auctions and that of monopoly pricing; “the analysis of optimal auctions is essentially equivalent to the analysis of standard monopoly third-degree price discrimination” (Bulow and Roberts, 1989). The auction problem can therefore be understood by applying the usual logic of marginal revenue versus marginal cost. Bulow and Roberts (1989) show that under the assumptions of the RET the expected revenue from an auction equals the expected marginal revenue of the winning bidder(s).

So in an optimal auction the objects are allocated to the bidders with the highest marginal revenues, just as a price-discriminating monopolist sells to the buyers with the highest marginal revenues (by equalizing the lowest marginal revenues sold to across different markets). And just as a monopolist should not sell below the price where marginal revenue equals marginal cost, so an auctioneer should not sell below a reserve price set equal to the value of the bidder whose marginal revenue equals the value to the auctioneer of retaining the unit. The marginal revenue should be set equal to zero if the auctioneer, or monopolist, is simply maximizing revenues. Under the assumptions of the RET, and if bidders with higher signals have higher marginal revenues, *all the standard auctions are optimal if the seller imposes the optimal reserve price* (Klemperer, 2004).

## 5.2 Assessment and Recommendations for Pakistan’s Mechanism

The following assessment is based primarily on a paper by Harris and Raviv (1981), who derive the form of an optimal marketing scheme in the context of a monopolistic seller, producing a homogenous product, with and without capacity limitations.

They assume unit demand for any price at or below a buyer's reservation price.<sup>1</sup> They also assume buyers are identical except for their reservation price and asymmetric (ie, each buyer knows her known reservation price and not that of any other).<sup>2</sup>

Their model closely matches that for the sale of hunting permits by the Balochistan wildlife department. That is, the wildlife department is the monopolistic seller producing hunting permits (homogenous product), with an exogenous capacity limit. The capacity limit is considered exogenous because it is dependent on the Markhor population that is obviously not determined (at least not completely) by the department (or anyone else). I assume that the individual demand for permits is unit, largely because of hunters' characteristics. That is most hunters interested in such expensive and rare trophies usually desire just one, because of (i) the cost, and (ii) the value of a second trophy declines significantly once one is obtained.

Clearly, if the department had complete information about the reservation price of each bidder, it would be optimal for it to sell one unit each to buyers with the highest reservation price and to charge each buyer her true reservation price (ie, perfect price discrimination). In the absence of such complete information, it is not possible to perfectly discriminate, but is possible to discriminate to some extent (Harris and Raviv, 1981). Harris and Raviv (1981) show that there are two optimal pricing schemes when the available quantity of the object (hunting permits) is exogenously determined, and less than the number of potential bidders.

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<sup>1</sup>It must be clarified that this unit demand is an individual bidder's demand, and not the combined (or market) demand for permits.

<sup>2</sup>The authors also apply the *revelation principle* to the mechanisms, implying direct and truthful schemes. They define a direct scheme as one in which each buyer writes down a bid or declared price without knowing what other buyers are writing. A truthful scheme is defined as an direct scheme in which the buyer's optimal strategy is to declare her true reservation value, given that all other buyers are also declaring their true reservation values.



First, they prove that a “priority pricing” scheme is optimal for all parameters of their model. Such a scheme is one in which the seller announces a schedule of prices, and each potential buyer chooses a priority price, which she is willing to pay. The key point here is that buyers choosing higher prices expect and must receive a better “version” of the product. For example, electricity and natural gas is sold to some industrial customers using a priority pricing scheme, and customers paying lower prices are cut off before those paying higher prices in times of shortage. Since the hunting permits are homogeneous, the priority pricing scheme will only be feasible and optimal for the department if it can somehow convert a homogeneous product into a heterogeneous one. This is not as difficult as it may seem. For example, hunters choosing higher prices may be given first-access to the hunting area, ie, the highest bidder be given first access, the second highest second access, and so on. The higher bidders may also be given more days to complete their hunt. Thirdly, if the hunt is unsuccessful because a hunter missed her shot, the higher bidders may be given a refund or a return opportunity, that is currently denied under the existing mechanism. Thus, a seemingly homogeneous product can be made heterogeneous in order to successfully apply a priority pricing scheme.

Second, Harris and Raviv (1981) also prove the optimality of a common price auction with minimum acceptable bid, which they call a *Modified Vickrey Auction*. The modified auction differs from the Vickrey auction in two ways. First, it includes a minimum acceptable bid, and second, the discreteness of the possible reservation prices is exploited by sometimes setting the price above the highest rejected bid. They show that such an auction is not always feasible<sup>3</sup>, but is always optimal when it is feasible.

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<sup>3</sup>In some cases, the conditions applied to this mechanism require a successful bidder to pay more than her endowment, which is obviously not possible, and therefore not feasible.

In addition to an exogenous capacity limit, Harris and Raviv (1981) consider the case where capacity may be endogenously determined. For the Balochistan wildlife department this is a possibility if population numbers are significantly high. In such a case, they show that if increasing capacity is costless, then choosing capacity equal to the potential demand and setting a single price is optimal. For the Markhor, this increase in capacity is equivalent to the hunting of a greater number of animals, and this may be viewed as a cost if this negatively affects their population dynamics. Thus, Harris and Raviv (1981) state that if increasing capacity is at all costly, then setting capacity to be less than potential demand and using priority pricing or the modified Vickrey auction are optimal.

Based on the review above, I would recommend a change in the delivery mechanism from a first-price sealed-bid auction to either the priority-pricing or modified Vickrey auction. Additional advantages of a modified Vickrey auction (and other sealed-bid auctions) are that such auctions are generally more attractive to entrants. Furthermore, the Vickrey auction, because it encourages “truth-telling” (buyers will state their true values as a dominant strategy), will not discourage potential bidders who have only small amounts to trade (Klemperer, 2004).

Though the problem of collusion is unlikely since the bids are submitted by both national and international hunters from all over the world, thus for all to collude would take considerable resources and organizational ability, which is highly unlikely. Collusion is usually harder in sealed-bid auctions than ascending auctions in any case (Klemperer, 2004). Lastly, though I assumed private-values, in the common values case in which bidders have similar actual value for a prize, the “winners curse”<sup>4</sup> problem for a weaker bidder is far less severe in a sealed-bid auction.

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<sup>4</sup>In short, the winner’s curse says that in such an auction, the winner will tend to overpay.

### 5.3 Complete Information

In this section I carry out an analysis of the optimal strategy and resultant population dynamics in the presence of complete information that would allow the wildlife department to discriminate perfectly. I assume zero marginal costs and a downward sloping linear demand curve. Varying the slope changes the static revenue maximizing quota, which, if the demand curve is given by  $p(q) = a - bq$ , is calculated as  $q = \frac{a}{2b}$ . I assumed that quantity demanded would fall to zero if permits were priced at  $\geq \$100,000$ .

The slope of the demand curve is directly related to the concept of price elasticity of demand, which may be written mathematically as:

$$\eta = \left| \frac{\frac{\delta q}{q}}{\frac{\delta p}{p}} \right| \quad (5.1)$$

The inverse of the price elasticity of demand, ie, the flexibility of price to changes in quantity is then:

$$f = \left| \frac{\frac{\delta p}{p}}{\frac{\delta q}{q}} \right| = \frac{1}{\eta} \quad (5.2)$$

Figures 5.1 to 5.8 below show the revenue maximizing quota and revenues from varying the slope of the demand curve. The harvest dynamics (for both proportional and constant harvest) of  $\geq 6$  year old males corresponding to the revenue maximizing quota is also shown. Based on the analysis in the following figures therefore, in order to maximize realized revenues, the monopolist should set a larger quota if  $f < 1$  ( $\eta > 1$ ), and a smaller quota if  $f > 1$  ( $\eta < 1$ ).

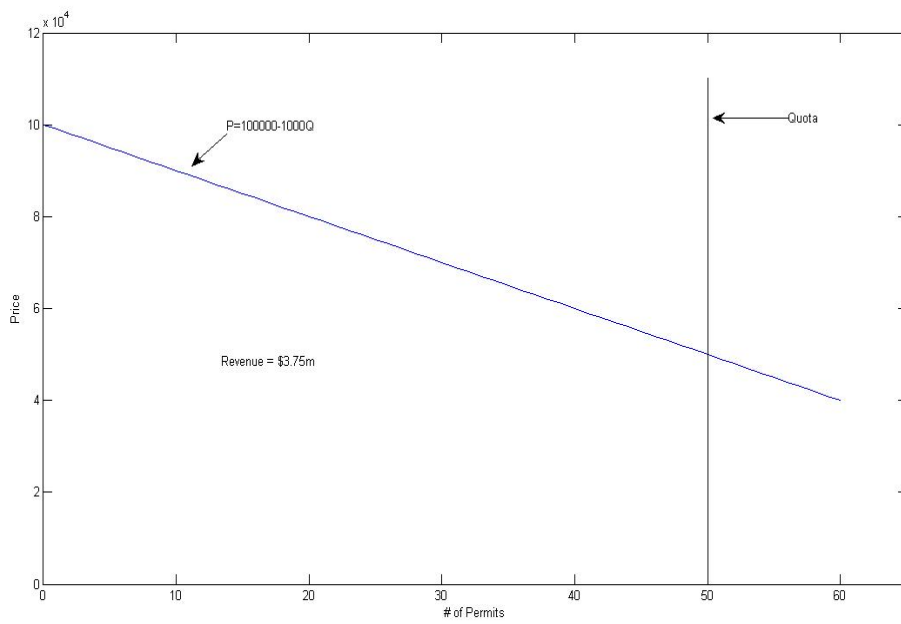


Figure 5.1: Perfect Price Discrimination A

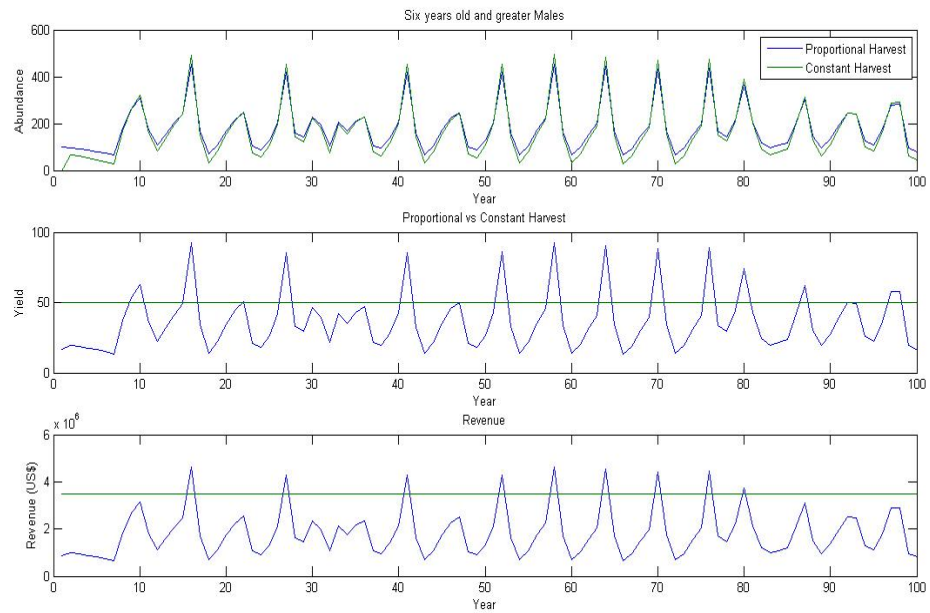


Figure 5.2: Dynamics with a harvest of 50 (18%) of  $\geq 6$

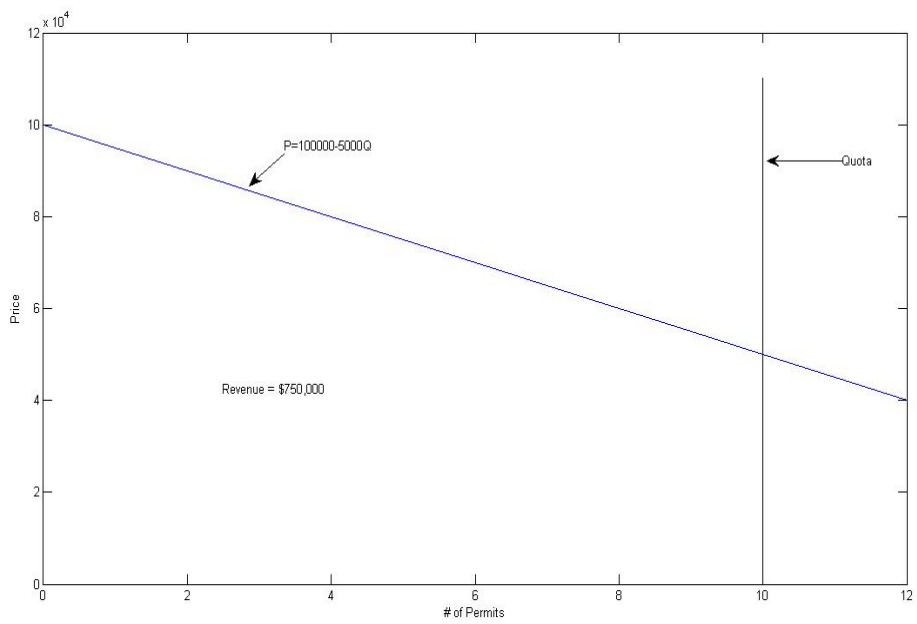


Figure 5.3: Perfect Price Discrimination B

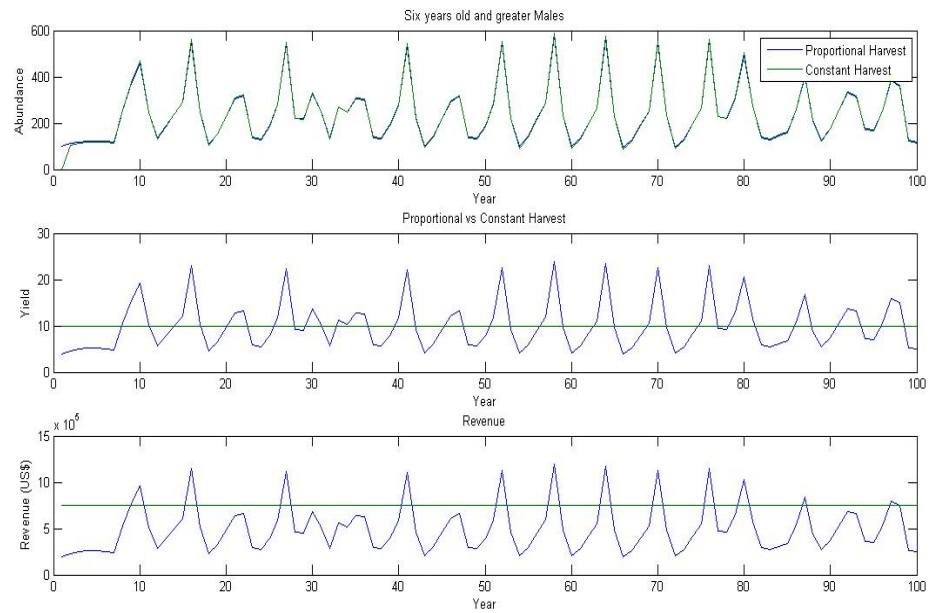


Figure 5.4: Dynamics with a harvest of 10 (4%) of  $\geq 6$

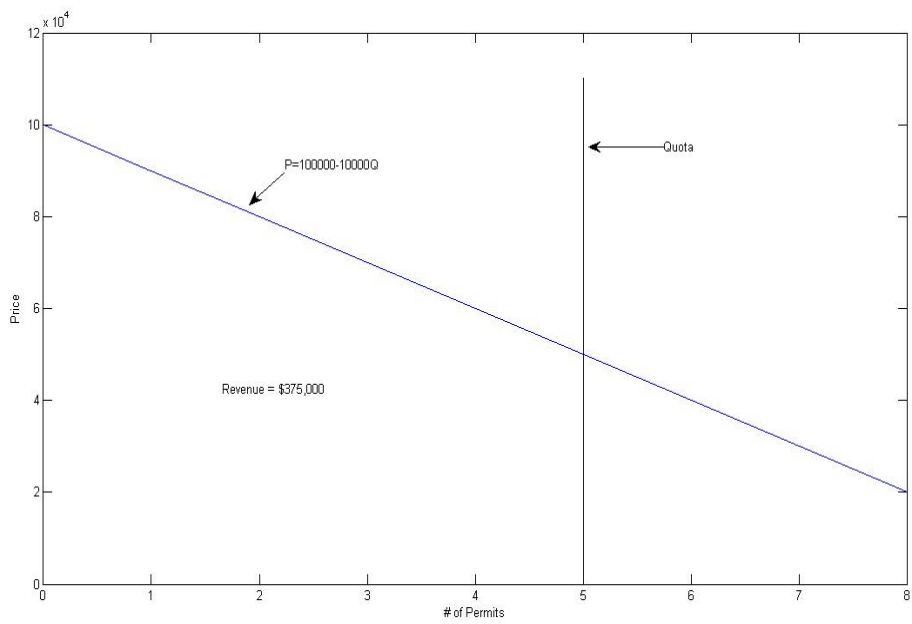


Figure 5.5: Perfect Price Discrimination C

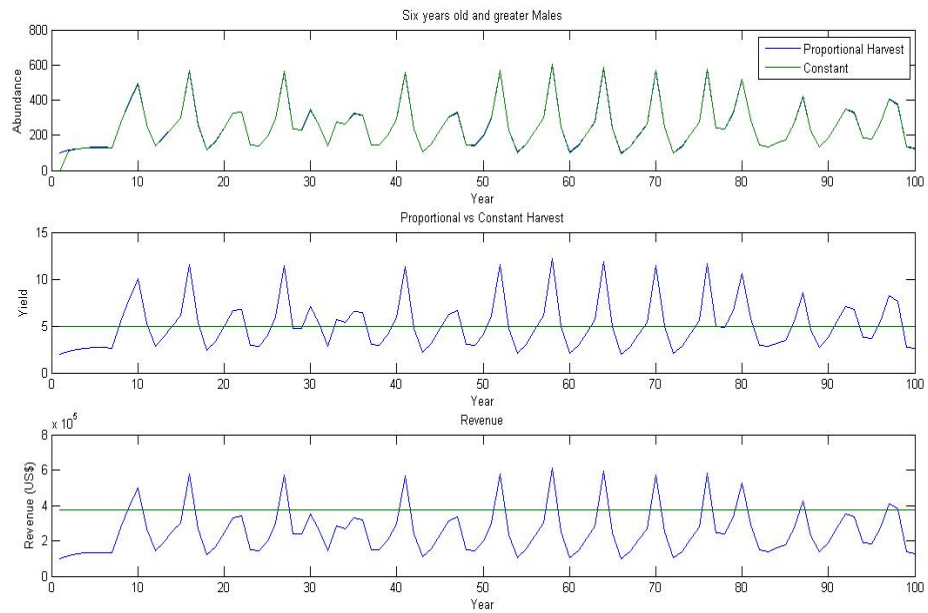


Figure 5.6: Dynamics with a harvest of 5 (2%) of  $\geq 6$

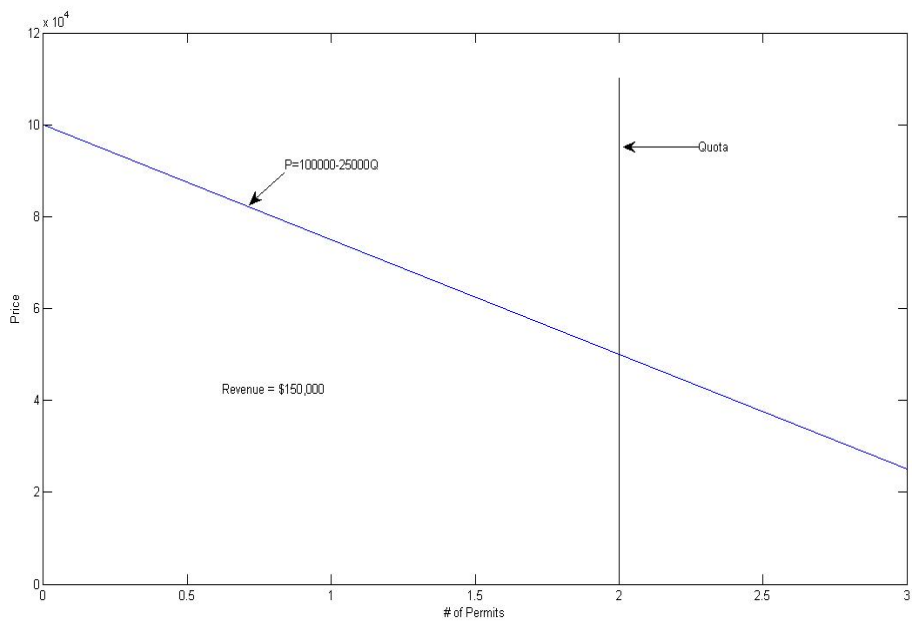


Figure 5.7: Perfect Price Discrimination D

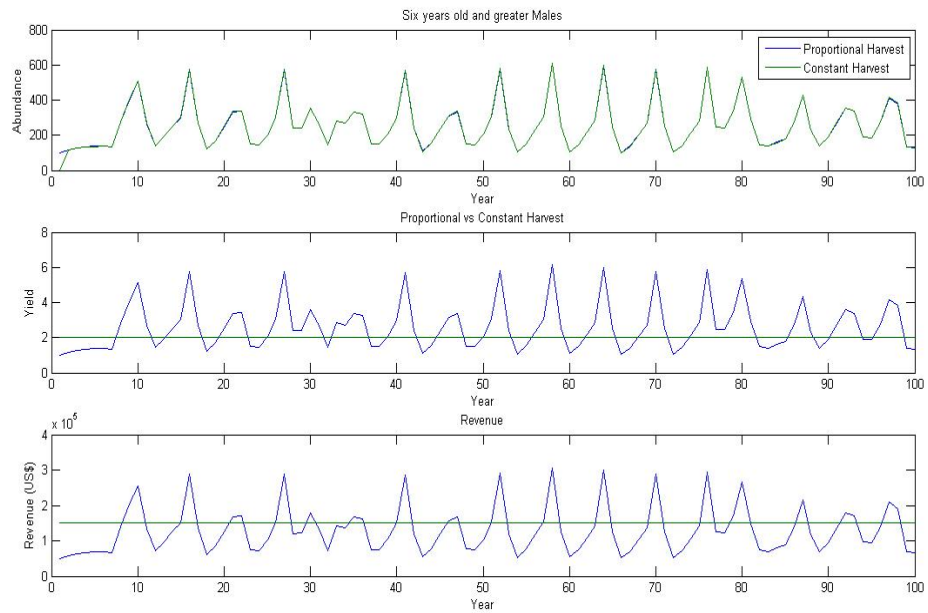


Figure 5.8: Dynamics with a harvest of 2 (1%) of  $\geq 6$

As mentioned in section 4.2.2, harvest of up to ninety percent of the  $\geq 6$  years old males does not affect the overall population dynamics of the Markhor. Therefore, at first it appears that all the revenue maximizing quota levels derived above are biologically sustainable. However, as mentioned in 2.1.2, there are negative evolutionary consequences of trophy hunting such as reduced horn sizes and body weight resulting from hunting the largest trophies trophies. Shackelton (2001) states “evidence suggests that in the short term, there are few if any negative effects of trophy hunting, which is to be expected if the majority of mature males are not hunted. What is unknown however, is the long-term genetic impact of this activity, because trophy hunting removes what are most probably the genetically superior individuals from a population”. Again, the impact will likely be minimized if only a fraction of the mature trophy males are taken each year.

Thus, if the wildlife department has complete information about hunters’ reservation prices, and can construct a market demand curve from individual preferences, it is possible to perfectly discriminate amongst the hunters and maximize revenue. However, the quota allocation decision has to be made in combination with theory and models from population and evolutionary biology in order to ensure sustainability.



## CHAPTER 6

### CONCLUSIONS

The main objective of this thesis was to model and simulate two-sex population dynamics, with harvest, in order to assess the conditions under which harvest might be biologically sustainable. It was also an attempt at addressing some of the criticisms of bio-economic models by considering ecological complexity in a revenue maximizing trophy harvest model. Prior to my research, it was not clear how trophy hunting of a small percentage of mature adult males affected the population dynamics of the Markhor population in western Pakistan. Anecdotal evidence seemed to suggest that the population was not adversely affected. My research therefore, based on a more scientific analysis, was aimed at either bolstering that view or negating it. As it turned out, the anecdotal evidence holds up in the face of my research on the population dynamics of the trophy hunted Markhor.

The main questions I had hoped to answer were:

1. Are current recommendations of a 2 to 5 percent offtake biologically sustainable?
2. Is targeting a specific age or sex class biologically sustainable?
3. What combination of permit price and quota allocation maximizes revenue, and under what conditions?
4. What is the optimal delivery mechanism for the sale of hunting permits?

Given the structure of the biological model, a 2 to 5 percent offtake is biologically sustainable. In fact, an even higher offtake, at first glance, appears not to

alter population dynamics. The model also demonstrated that a certain percentage of female offtake and/or multiple age classes may also be harvested without significantly altering population dynamics.

It is noteworthy that management options usually include targeting males, both because of their larger size and potential for trophy hunting, and for the sake of sparing females to produce young. But Rankin and Kokko (2007) suggest that “such a management strategy may push the sex ratio at which maximal offspring production occurs very close to the threshold under which females become unable to find a mate, reducing the population density to dangerously low levels”, such as in the Saiga antelope. There are many instances where the removal of males appears to have little effect on population persistence, indicated by examples such as extreme sex ratio bias in the face of male killing, or the simple observation that populations subjected to selective harvesting of males can be sustainable if it is not excessive. However, persistence does not mean that population growth has not been impacted, and a dearth of males may cause a reduction in average female fecundity (Rankin and Kokko, 2007). Additionally, the loss of genetically superior animals (ie, larger horn size is not just age related, but also implies greater fitness), and the negative evolutionary consequences associated with this must be taken into account when devising harvest management strategies.

In the absence of complete information, it was shown that the existing delivery mechanism (ie, a first-price sealed-bid auction), with capacity limitations that are exogenously determined, is not optimal. A priority pricing or second-price sealed bid auction are more likely to maximize the wildlife department’s expected revenues.

In the presence of complete information however, we assume we know each

potential bidder's reserve price, and therefore charging each bidder her reserve price would be optimal (ie, perfect-price discrimination). In order to maximize realized revenues in such a case, the monopolist should set a larger quota if  $f < 1$  ( $\eta > 1$ ), and a smaller quota if  $f > 1$  ( $\eta < 1$ ) (see equations 5.1 and 5.2). Without knowing the functional form of the demand curve for hunting permits however, it is difficult to conjecture what specific combination of permit price and quota allocation would maximize revenue. An accurate estimation of this relationship was beyond the scope of this thesis, but would be a topic for future research. This may be done by collecting information on the value and number of bids submitted, as well as questionnaires designed to elicit the hunters' willingness to pay for permits, which could help in applying contingent valuation techniques to estimate the demand for permits.

The paper has also pointed out the necessity of certain data for an accurate application of the model. The vital rates in particular, should ideally be estimated from long-term data for the specific species being simulated, as opposed to inferring them from similar species. In addition, the functional form of the model used in this thesis treated the entire population as one single herd. Data on specific herds, and dispersal among herds would enable a more accurate dispersal model to be formulated. Incorporating data on weather, forage availability, and the introduction of a stochastic component to capture random drift would also bring the model closer to mimicking the actual conditions facing the population of the Markhor, and would likely be more accurate in simulating the population dynamics.

It is hoped that the methods and model developed in this thesis may be used by planners and managers as a framework to make quota allocation and permit pricing decisions while maintaining sustainable harvest programs for various species. It is

also hoped that this thesis will serve as a guide for data collection needs for an accurate prediction of the impact of trophy hunting on population dynamics.

# APPENDIX A

## FORMULAS

Fecundity:

$$\begin{aligned}
 F_4 = & \frac{(k_{49}M(n_4, n_9)h_9^{-1}) + (k_{410}M(n_4, n_{10})h_{10}^{-1})}{n_4 + D_1(n_5 + n_6 + n_7)} \\
 & + \frac{(k_{411}M(n_4, n_{11})h_{11}^{-1}) + (k_{412}M(n_4, n_{12})h_{12}^{-1})}{n_4 + D_1(n_5 + n_6 + n_7)} \\
 & + \frac{(k_{413}M(n_4, n_{13})h_{13}^{-1})}{n_4 + D_1(n_5 + n_6 + n_7)} \quad (\text{A.1})
 \end{aligned}$$

$$\begin{aligned}
 F_5 = & \frac{(k_{59}M(n_5, n_9)h_9^{-1}) + (k_{510}M(n_5, n_{10})h_{10}^{-1})}{n_5 + D_2(n_4 + n_6 + n_7)} \\
 & + \frac{(k_{511}M(n_5, n_{11})h_{11}^{-1}) + (k_{512}M(n_5, n_{12})h_{12}^{-1})}{n_5 + D_2(n_4 + n_6 + n_7)} \\
 & + \frac{(k_{513}M(n_5, n_{13})h_{13}^{-1})}{n_5 + D_2(n_4 + n_6 + n_7)} \quad (\text{A.2})
 \end{aligned}$$

$$\begin{aligned}
 F_6 = & \frac{(k_{69}M(n_6, n_9)h_9^{-1}) + (k_{610}M(n_6, n_{10})h_{10}^{-1})}{n_6 + D_3(n_4 + n_5 + n_7)} \\
 & + \frac{(k_{611}M(n_6, n_{11})h_{11}^{-1}) + (k_{612}M(n_6, n_{12})h_{12}^{-1})}{n_6 + D_3(n_4 + n_5 + n_7)} \\
 & + \frac{(k_{613}M(n_6, n_{13})h_{13}^{-1})}{n_6 + D_3(n_4 + n_5 + n_7)} \quad (\text{A.3})
 \end{aligned}$$

$$\begin{aligned}
F_7 = & \frac{(k_{79}M(n_7, n_9)h_9^{-1}) + (k_{710}M(n_7, n_{10})h_{10}^{-1})}{n_7 + D_4(n_4 + n_5 + n_6)} \\
& + \frac{(k_{711}M(n_7, n_{11})h_{11}^{-1}) + (k_{712}M(n_7, n_{12})h_{12}^{-1})}{n_7 + D_4(n_4 + n_5 + n_6)} \\
& + \frac{(k_{713}M(n_7, n_{13})h_{13}^{-1})}{n_7 + D_4(n_4 + n_5 + n_6)} \quad (\text{A.4})
\end{aligned}$$

$$\begin{aligned}
F_9 = & \frac{k_{49}M(n_4, n_9) + k_{59}M(n_5, n_9)}{n_9h_9^{-1} + D_5(n_{10} + n_{11} + n_{12} + n_{13})} \\
& + \frac{k_{69}M(n_6, n_9) + k_{79}M(n_7, n_9)}{n_9h_9^{-1} + D_5(n_{10} + n_{11} + n_{12} + n_{13})} \quad (\text{A.5})
\end{aligned}$$

$$\begin{aligned}
F_{10} = & \frac{k_{410}M(n_4, n_{10}) + k_{510}M(n_5, n_{10})}{n_{10}h_{10}^{-1} + D_6(n_9 + n_{11} + n_{12} + n_{13})} \\
& + \frac{k_{610}M(n_6, n_{10}) + k_{710}M(n_7, n_{10})}{n_{10}h_{10}^{-1} + D_6(n_9 + n_{11} + n_{12} + n_{13})} \quad (\text{A.6})
\end{aligned}$$

$$\begin{aligned}
F_{11} = & \frac{k_{411}M(n_4, n_{11}) + k_{511}M(n_5, n_{11})}{n_{11}h_{11}^{-1} + D_7(n_9 + n_{10} + n_{12} + n_{13})} \\
& + \frac{k_{611}M(n_6, n_{11}) + k_{711}M(n_7, n_{11})}{n_{11}h_{11}^{-1} + D_7(n_9 + n_{10} + n_{12} + n_{13})} \quad (\text{A.7})
\end{aligned}$$

$$\begin{aligned}
F_{12} = & \frac{k_{412}M(n_4, n_{12}) + k_{512}M(n_5, n_{12})}{n_{12}h_{12}^{-1} + D_8(n_9 + n_{10} + n_{11} + n_{13})} \\
& + \frac{k_{612}M(n_6, n_{12}) + k_{712}M(n_7, n_{12})}{n_{12}h_{12}^{-1} + D_8(n_9 + n_{10} + n_{11} + n_{13})} \quad (\text{A.8})
\end{aligned}$$

$$F_{13} = \frac{k_{413}M(n_4, n_{13}) + k_{513}M(n_5, n_{13})}{n_{13}h_{13}^{-1} + D_9(n_9 + n_{10} + n_{11} + n_{12})} + \frac{k_{613}M(n_6, n_{13}) + k_{713}M(n_7, n_{13})}{n_{13}h_{13}^{-1} + D_9(n_9 + n_{10} + n_{11} + n_{12})} \quad (\text{A.9})$$

Where,

$$M(n_i, n_j) = \frac{2n_i n_j}{n_i + n_j} \quad (\text{A.10})$$

$h_i$  represents harem size and is used to incorporate polygyny in to the model. For monogamous mating systems, this may simply be dropped from the fecundity equations above.

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