

## Animal Rationality and Implications for Resource Management – The Case of Biological Reserves for Moose and Pine.

**Synopsis.** One logical implication of the Darwinian hypothesis of ‘survival of the fittest’ is that animals exhibit optimizing behavior. Surprisingly, this has not been included in the resource economics literature. This paper explores the implications of optimizing behavior in a model where moose face migration decisions and humans wish to keep moose out of an area to protect young pine trees. The results show that if moose are rational, a given hunting effort will lead to better outcomes for humans than if the moose only focus on harvesting opportunities. This finding suggests that the validity of the standard assumption that animal migration behavior is density-dependent should be re-examined.

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## Introduction

The purpose of the present paper is to demonstrate by example that assumptions about animal behavior are important in the practical regulation of natural resources. A considerable part of the field of resource economics is devoted to the *economic management of living organisms* (EMLO).<sup>1</sup> Any student of resource economics receives training in the integration of biological and economic models. See for instance, Hanley et al. (1997), Perman et al. (2003). Many resource economists collaborate with biologists in their areas of research. It is therefore surprising that organism adaptation to human use of living natural resources has received very little attention in the EMLO literature. The idea that animals exhibit optimizing behavior is central to any modern textbook on the subject, Krebs & Davies (1993), Drickamer et al. (2002). To the author's best knowledge, resource economists have been slow in incorporating these results into their models. Rather, economists have treated animals<sup>2</sup> as automata that are behavioral dummies. This is implied by the use of standard models, like Schaeffer and Gompertz-growth models and Volterra-Lotka-type predator-prey relationships. See Clark (1976) for a review. These models, intended to be parameterizations of an underlying, unknown growth process, may capture the essentials of the dynamics involved, and may therefore be appropriate in some cases.<sup>3</sup> In other cases, however, one could argue that animal rationality is important. As far as the author is aware, only two papers have explicitly incorporated optimizing behavior in

animals into resource economic models. These papers, Finnoff & Tschirhart (2003a, 2003b), examine harvesting in an eco-system when animals maximize their net energy intake. The analysis in these papers represents a major step forward, but does not take into account the fact that net energy intake is but one of the variables that determines reproductive success. If other variables are important, then they are also expected to affect animal behavior, as reproductive success forms the relevant objective function.

The apparent failure of the EMLO literature to incorporate assumptions about optimizing organisms is even more surprising given that biology and economics are, in many ways, closely related disciplines. Indeed, they are both concerned with the individual achievement of specified objectives and how this is affected by resource scarcity, Ghiselin (1978, 1995). In both fields, the adaptive response to scarcity gives rise to aggregate mechanisms for how resources are distributed. These mechanisms for distribution are functions of the interaction between individuals and usually described in terms of competition, cooperation, and conflict, Hirshleifer (1978). The similarities between the fields have led to the development of a similar nomenclature with terms like costs, benefits and trade-offs being common to both; see Chapter 3 in Krebs & Davies (1993). There are also many similarities in the use of modeling tools and the fields have learnt much from each other. Dynamic optimization techniques that have long been ubiquitous in economics are now used to study animal behavior, Mangel & Clark (1988). For example, the

equilibrium concept of Evolutionary Stable Strategies first developed in ecology, Smith & Price (1973), is now used in economics, Weibull (1995). A recent example of fruitful interaction between the fields is the development of 'neuroeconomics' as a distinct field incorporating assumptions and results from neuroscience into economic models, Camerer et al (2005). Indeed, the similarities between the fields are such that '...it is fairly easy to switch from one field to another,' Tullock (1979). Of course, the fundamental unifying principle of biology and economics is optimization. The idea that an organism, in some way or another, adapts to its environment in order to maximize its reproductive success is strikingly similar to the idea that a human allocates available resources in order to maximize utility. One would therefore expect that when economists model the interaction of humans and other organisms, mutual adaptation would lie at the forefront of modeling. Unfortunately, this does not appear to be the case.

The question raised here is whether rationality, as a driving force for animal behavior, has any serious implications for the management of wildlife resources.<sup>4</sup> In particular, the paper examines whether animal rationality has implications for the economic and biological efficiency of Biological Reserves (BRs). BRs are established for a number of reasons, but one of the most common is to provide a sanctuary for wildlife where they can breed while sheltered from human activity. Part of the rationale for BRs is also that by providing habitat in a designated area human activity, such as agriculture, may be protected from the harmful consequences of the behavior of

certain species. For example, in Norway it has been suggested that habitat reserves for predators such as wolves be established while simultaneously allowing more or less unregulated hunting of the predator outside the BR where the predator preys on domesticated animals. For terrestrial reserves, the economic literature is smaller. However, one candidate study is Skonhofs et al (2002) examination of the management of migrating chamois. This study assumes density-dependent migration and concludes that economic inefficiency is large when migration rates are high. The relationship between the migration rate and economic efficiency is obtained through a simulation based on the estimated parameters. The results in Skonhofs et al (2002) hinges crucially on the assumption of density-driven migration. There is a somewhat larger economic literature on marine BRs. This literature appears to be more critical of their efficiency, Sanchirico & Wilen (1999), Holland (2000), Sanchirico & Wilen (2001), and Hannesson (2002). The adaptive behavior of fishermen/women is one reason, but another is that as fish are harvested in one area, they will migrate from the BR to unprotected areas and would then be inefficiently harvested unless the fisheries outside the BR are subject to some kind of regulation. It is worthwhile to point out that this conclusion depends on the assumption that fish stock migration is driven by density dependency, and that alternative determinants of migration behavior may lead to different results. Hannesson (2002) and Sanchirico & Wilen (1999) implicitly acknowledge this for the case where the different areas may be categorized as either sinks or sources. Sanchirico et al (2006) examines when the establishment of marine BRs is optimal and

point out that assumptions about migration are important as they determine whether a reserve will be a sink or a source. In contrast to the economic literature, biologists often conclude from an ecological perspective that BRs are generally effective instruments for protecting marine ecosystems and/or single species populations within the reserve, Gell & Roberts (2002), Palumpi (2003).

In the current paper, we examine a particular type of BR where moose are protected from hunting in one BR while young pine trees are protected from moose foraging by hunting in an adjacent area. In one area, moose forage on a resource that has no economic value. In the other, they forage on young pine trees and damage the economic value these trees will have when harvested, Edenius et al (2002). Since both trees and moose are valuable resources, we would ideally like to have ‘many’ moose where they do no damage and ‘few’ where they forage on pine. The economic regulation of moose foraging on resources where value has a spatial distribution has been analyzed by Bergland et al (2006) and Wam et al (2005). Both of these articles apply a density-dependent model of moose migratory behavior. In this paper, the effect of different assumptions about the determinants of migration patterns is analyzed. It is shown that if animals take the risk of hunting into account, many of the conclusions drawn from density-driven models are reversed. As reviewed in the following section, there is ample empirical evidence in

the biological literature that animals, particularly moose, respond to predatory pressures by altering their behavior.

## **1. Rationality in animal behavior**

As in economics, optimizing behavior is a fundamental principle underlying much of the scientific analysis of animal behavior. Indeed, this journal has published a number of papers exploring the implications of economic modeling on biological problems. For instance, Cassill (2003) considers the reproductive efforts of the ant queen in a capital-theoretic framework and Landa & Tullock (2003) attribute the differences in nesting practices of bees and ants to a cost-benefit calculation wherein the benefits of establishing satellite nests by bees are less because bees fly. Even in papers that aim to establish differences between humans and primates, the underlying idea that behavior is somehow rational and related to economic reasoning is always present (see Pryor 2003, Boehm 2004). The main difference between economics and the study of animal behavior is that economists usually pay very little attention to the translation of the solution of an optimization problem into a description of a process that produces behavior consistent with optimization. This is of utmost importance in the study of animal behavior.

The key is *selection* and the insight that selection works on a genetic level, Dawkins (1976). Here, the function of genes is to code for the synthesis of proteins. Proteins regulate the physical development of an organism, as well as the behavior of that organism. The selection mechanism favors genetically determined strategies that have a higher likelihood of survival in reproduction and crowd-out less successful strategies. In this view, organisms are little but vessels for genes. The genes affect behavior by producing proteins, and the most successful genes replicate themselves. There is, in principle, very little difference between what constitutes selection for a physical trait and selection for a given behavior. For example, polar bears are white because at some point in time bears with relatively little pigmentation in the fur had a higher probability of reproducing than other bears in the same habitat. However, while white fur on polar bears is a physical trait, consider instead the extremely sophisticated behavior of the cuckoo. Cuckoos lay their eggs in the nests of other birds because at some point in time and in some species of bird this behavior gave the birds in question an edge with respect to reproductive success, Davies (2000). At some other point in time, some newly-hatched bird started throwing the eggs of potential (step)siblings out of the nest. This behavior also increased the probability of reproduction and the gene(s) responsible for this behavior proved more successful than other gene combinations. Note that the behavior of cuckoos must be genetically determined. There simply is no possibility of learning this behavior from other cuckoos and it seems rather farfetched to believe that cognitive processes would lead to the same behavior in all individuals.

There is a small economic literature on the management of resources in the presence of genetic selection mechanisms. For instance, Laxminarayan & Brown (2001) and Munro (1997) model the economic management of the evolution of resistance to pathogens and conclude that failure to consider selection may lead to sub-optimal decisions.

Seemingly, there is no room for learning or conscious decision-making and problem solving in this setup.<sup>5</sup> However, both the ability to learn and the ability for conscious decision-making are traits that can be selected for. The ability to learn is well documented in a large number of species, such as fruit flies that learn to associate certain smells with electric shocks, Dudai & Quinn (1980). Whether animals engage in conscious decision-making appears to be controversial, see the introduction to Bekoff et al (2002). Some studies appear to explore this possibility whereas others insist on explaining behavior as strategies surviving the selection process. It does appear that most ecologists accept that large mammals have sufficient cognitive ability to change their strategies in response to changes in the environment. The following quote from an ecology article on animal adaptation to human activity is quite representative: ‘A vast literature supports the hypothesis that anti-predator behavior has a cost to other activities, and that this trade-off is optimized when investment in anti-predator behavior tracks short-term changes in predation risk,’ Frid & Dill (2002). There is a mounting body of research that is

generally interpreted as providing evidence of cognitive ability in animals. See Griffin & Speck (2004) for a review.

When studying BRs and their efficiency, we consider the foraging, migratory and population dynamic response to geographic variations in predatory pressure. The ability of animals to make their own foraging strategies contingent on predator pressure has been documented over the entire spectrum of presumed animal cognitive ability. Crustacean zooplankton, Neill (1990), and primates, Miller (2002), are just two examples, each located at different ends of this spectrum. The main insight from this literature is that animals weigh the risks of being eaten against the benefits of foraging, and that strategies are chosen that appear to recognize this trade-off and respond to it in a manner consistent with optimizing behavior. In particular, animals respond to predation by humans. Slobodchikoff (2002), for instance, considers prairie dogs and finds that prairie dogs have distinct alarm calls, risk-assessment, and escape strategies for different predators and that humans are one of the predator species worthy of a distinct behavioral pattern. An example of perhaps somewhat greater urgency to resource economists is the adaptation to selection pressures in fisheries, Favro et al (1979). Here selection pressure caused by harvesting has been so massive that it has been suggested that both behavioral and physical adaptations have occurred. Although most of the adaptation is on the morphological<sup>6</sup> level, there is also experimental evidence that suggests that fish have a

substantial ability to learn how to avoid capture, Brown & Warburton (1999). In a study by Heino & Godø (2002), the behavioral adaptations examined include the increased alertness towards harvesting equipment, the increased spread of the seasonal spawning period and the spatial dispersal of the fish population. All of these adaptations come with a fitness cost in the sense that they make the animals less adapted to their natural environment and therefore reduce the intrinsic growth rate.

The current paper deals with adaptive behavior in moose. There is considerable evidence that ungulates, including moose, respond behaviorally to increased natural predation pressures. Ripple & Beschta (2006) and White & Feller (2001), for instance, show that elk foraging patterns respond to the presence of carnivores (wolves). Bowyer et al (1999) and White & Berger (2001) present evidence that female moose a trade-off between foraging and other activities to lower the risk of predation. The effect of human hunting on moose behavior is less well documented. Baskin *et al* (2004) report numerical estimates of the geographical distance that a moose will cover in order to escape hunters and finds that the response is different for males and females. This study also cites an older Russian study where the escape behavior of moose depends on local hunting pressure, Glushkov (1976). A study that investigated the effect of hunting on moose reproduction gives an indication that human hunting affects habitat selection. Laurian et al (2000) examined two geographically close areas in Quebec with similar foraging opportunities.

Predation mortality caused by carnivorous predators was estimated to be of little importance in both areas. In one area, moose hunting had been banned for thirteen years before and during the study. In the second area, hunting had historically been allowed with an estimated harvesting rate of 15-20% before and during the study. The study was conducted over the period 1994-1997. For the entire period, the moose density was consistently *three* times higher in the area with no hunting. Although it is difficult to disentangle the direct effects of hunting from the effects of predator avoidance, it appears reasonable to conclude that the large difference in densities was partly caused by predator avoidance. At any rate, the large difference is not compatible with density-dependent migration from the area with no hunting.

## **2. A Model of migration in moose that forage on young pine trees**

A model is examined where moose may migrate between two areas. Except where moose would be considered averse to hunting risk, the model is very similar to the model in Wam et al (2005).<sup>7</sup> The stock of moose in Area 1 is denoted  $x_1$  and the stock of moose in Area 2 is denoted  $x_2$ . In the first area, they forage on some resource that is supplied in a fixed amount,  $K$ , per unit of time. In the second area, they consume the shoots of young pine trees,  $u$ , transforming undamaged young pine into damaged young pine,  $w$ , effectively making the tree economically less valuable when fully grown. The damage is proportional to the stock of moose in Area 1.

However, foraging does not damage older pine trees. Both damaged,  $z$ , and undamaged pine,  $y$ , contribute equally to the regeneration of young pine trees. At any point in time, fixed fractions of the young damaged and undamaged pine grow into damaged and undamaged grown pine respectively. Regeneration is assumed to be a logistic function of the sum of damaged and undamaged pine trees. It is further assumed that, in the absence of hunting and migration, the population dynamics for moose are determined by logistical growth in both areas. The following model describes the ecosystem:

$$\dot{x}_1 = rx_1 \left(1 - \frac{x_1}{K}\right) + \Phi \quad (1)$$

$$\dot{x}_2 = rx_2 \left(1 - \frac{x_2}{u}\right) - \Phi - h \quad (2)$$

$$\dot{u} = (z + y)(b - (z + y)) - \delta u - \alpha ux_2 \quad (3)$$

$$\dot{w} = \alpha ux_2 - \xi w \quad (4)$$

$$\dot{y} = \rho(y + \delta u)(G - (z + y)) - \beta y \quad (5)$$

$$\dot{z} = \rho(z + \xi w)(G - (z + y)) - \gamma z \quad (6)$$

$G, \rho, r, b, \delta, \beta, \gamma, \xi$  and  $\alpha$  are assumed to be positive constants. The net migration between the two areas is given by  $\Phi$ , and is discussed further below.  $h$  is the harvesting of moose.

While it is assumed that the population dynamics for moose are determined by logistic growth in both areas, the stocks of moose in both areas are adjusted by their migratory behavior. This system is too complicated to solve with analytical techniques, so the analysis is completed using numerical methods.<sup>8</sup>

It should be noted that migration is just one of the many complexities that arise in multiple species regulation, and that the model presented here is, in many respects, too simplistic. The analysis in Crépin (2003) shows that these complexities may give rise to non-concave dynamic analysis and multiple equilibria. Crépin's (2003) model does not include migration, focusing instead on more ecologically sophisticated differential equations that drive the growth of trees. These complexities have been suppressed in order to focus on the importance of animal rationality and its impact.

## **2.1. Animal rationality and migration**

If we believe that animals respond to changes in the environment, and that they do so in a way that either mimics optimizing behavior through genetic selection mechanisms or is the result of cognitive processes, then migration will obviously depend on the evaluation of the benefits of migration. The relevant objective function is to maximize reproductive success, often expressed as the expected number of surviving offspring. By assuming that reproductive success is a non-

decreasing function of expected energy intake, we can exchange reproductive success with energy intake as the objective function. We also need to incorporate the risk of death by hunting into the objective function. For economists, it is natural to apply the Von Neumann-Morgenstern axioms of decision-making under risk when forming the objective function. This framework has also been used by several ecologists, see e.g. Stephens & Krebs (1986) and the references therein. Expected utility theory allows the definition of a utility function where utility depends on energy intake,  $E$ . Thus, we assume that the utility of energy is given by:

$$U = U(E), U' \geq 0, U'' \leq 0 \quad (7)$$

One property of Von Neumann-Morgenstern utility functions that is very useful is that they are only determined up to an increasing linear transformation. Therefore  $U(E)$  is equivalent to  $AU(E) + B$ , where  $A$  is a strictly positive constant and  $B$  is any real number. Assume that there is some minimum energy intake,  $E^*$ , such that  $E \leq E^*$  indicates that the animal dies. By appropriate choice of  $A$  and  $B$  we can always define  $U(E^*) = 0$ . From the perspective of reproductive success, death by hunting should have the same value as death by starvation, so we can let the utility of being killed by hunters be equal to  $U(E^*)$ . The expected utility of consuming an energy amount  $E$  when there the risk of being hunted to death is equal to  $p$  is:

$$\mathbb{E}(U(E)) = (1-p)U(E) + pU(E^*) = (1-p)U(E) \quad (8)$$

Here  $\mathbb{E}$  is the expectations operator. An animal maximizing (8) or behaving as such, would exhibit rational behavior, at least as far as economists understand this concept. On the other hand, assuming that animals maximize  $U(E)$  implies that an animal is indifferent between two lotteries with pay-offs given by:

$$(1-p)U(E) \text{ and } (1-q)U(E), \quad p \neq q \quad (9)$$

This is inconsistent with rational behavior. However, this is exactly the assumption made when migratory behavior is assumed to be density-dependent.

For simplicity, we assume that animals are risk neutral. It should be pointed out that the empirical literature on risk sensitivity in animals presents clear evidence that animals have a considerably more nuanced attitude towards risk, and that risk-aversity appears to be the rule except when faced with severe resource scarcities, Caraco (1980), Caraco et al (1980), Real (1980). We formalize the distinction between rational and predator-sensitive moose behavior and purely density-driven moose behavior in the following manner:

**Density-driven migration behavior.** Here it is assumed that the animals can observe and compare the amount of food available, as well as the number of other moose in each area, before deciding where to settle. The animals' optimization problem is then:

$$\max \left( \frac{K}{x_1}, \frac{u}{x_2} \right) \quad (10)$$

$K/x_1$  is the amount of resources available per animal in Area 1.  $u/x_2$  is the amount of resources available in Area 2. Both these quantities are equal to the expected resource availability for an individual animal with pure density-dependent migratory behavior: the difference between them is assumed to drive migration. If  $K/x_1 > u/x_2$  the animal chooses Area 1. If  $K/x_1 < u/x_2$  Area 2 is optimal. If  $K/x_1 = u/x_2$ , then the animal is indifferent. If the decision-making process is not perfect, e.g. if migration takes time, the animals will not respond immediately. To capture this,  $\Phi$  is assumed to be given by:

$$\Phi = \phi \left( \frac{K}{x_1} - \frac{u}{x_2} \right), \phi > 0 \quad (11)$$

Here  $\phi > 0$  is a constant.  $\phi$  is a measure of how quickly the moose respond to ‘arbitrage opportunities’ by migrating. If  $\phi \rightarrow \infty$ , the moose will exploit differences in these opportunities infinitely quickly, and the system will always be in equilibrium in the sense that the net ‘utility’ will be the same in either area. Equation (11) represents migration as typically modeled in a density-dependent model.

**Migration behaviour based on expected utility maximization.** In this case, the moose understand that there is a probability of being killed by hunters. Thus, the animal weighs the availability of foodstuff with the risk of being killed. The animal is assumed able to monitor the hunting hazard through some mechanism such as the sound of gunshot or the smell of humans, dogs, carcasses, etc. The animals’ choice of area is then

$$\max \left( \frac{K}{x_1}, \left( 1 - \frac{h}{x_2} \right) \frac{u}{x_2} \right) \quad (12)$$

Here  $K/x_1$  is the expected resource availability per animal in Area 1 and  $\left( 1 - \frac{h}{x_2} \right) \frac{u}{x_2}$  is the expected resource availability in Area 2, adjusted for the risk of death. In this case  $\Phi$  is assumed to be:

$$\Phi = \phi \left( \frac{K}{x_1} - \left( 1 - \frac{h}{x_2} \right) \frac{u}{x_2} \right), \phi > 0 \quad (13)$$

From equation (13) it is clear that if there is no hunting, i.e. if  $h = 0$ , then equations (11) and (13) are identical. Conversely, if it is possible to hunt every animal that strays into Area 2, then any migration will always be towards Area 1, regardless of the availability of foodstuffs.

There is one aspect of migratory behavior in moose that is suppressed. Moose migration has a clear seasonal pattern where moose use foraging opportunities in different areas that vary over time. This could be incorporated into the analysis, e.g. by letting  $K$  be a time-dependent variable, and should not qualitatively affect the results, although the implications for practical resource management are considerable. Skonhøft & Olausson (2003) have analyzed the management of moose that exhibit seasonal migration. Another aspect that has been suppressed is that moose have more options for avoiding predation than migration. Here we focus on only the migration decision. Incorporating other dimensions of animal behavior would require that we drop the assumption of logistic growth and employ a substantially more complicated model.

A numerical simulation of the system without hunting is illustrated in Figure 1. Figure 1 shows that the variables exhibit dampened oscillations. The parameters in the model are

calibrated so that the steady state values of  $x_1$  and  $x_2$  are roughly equal to ten and the figure depicts the paths resulting from a perturbation relative to the steady state. Note that model includes the feature that the population dynamics of mature trees are slower than the dynamics of young trees and moose.

[Figure 1 about here]

Figure 1 also shows that some variables exhibit dampened oscillations whereas others converge monotonically. As the availability of young pine trees fluctuates, we would expect that migration patterns also fluctuate. This is indeed the case, as shown in Figure 2.

[Figure 2 about here]

## **2.2. The Effect of Hunting**

The effect of the attempt to reduce the number of moose in Area 2 may now be analyzed. First, we examine the case where a fixed number of animals are shot in each unit of time. The stock of moose in Area 2 is illustrated in Figure 3.

[Figure 3 about here]

From Figure 3 it is evident that hunting has the desired effect of reducing the stock of moose in Area 2, but that the effect is much larger if the moose decide on a migration based on expected utility, rather than solely on the foraging opportunities. Thus, hunting is a much more effective policy when migration is driven by expected utility. This is as expected. It is interesting to observe the stock of moose in Area 1. This is shown in Figure 4. From Figure 4 it is evident that when animals care about foraging opportunities alone, the introduction of hunting leads to the massive migration of moose from Area 1 to Area 2 because of the better foraging opportunities. Thus, the moose population in Area 1 decreases. However if the moose take the risk of being killed into account, the number of moose in Area 1 will approach a steady state with the same stock of moose as the case without hunting. Thus, the long-run moose stock in Area 1 is unaffected by the hunting in Area 2.

[Figure 4 about here]

We can briefly sum these findings as follows. If moose only care about foraging opportunities, trying to control the population leads to a ‘black hole’ effect where the shooting of animals is largely offset by the influx of animals from other locations. However, if animals take into account the risk of death, there is a ‘double dividend’ in the harvest since the surviving

animals are driven to areas where their presence is beneficial. This finding resonates with the literature on marine BRs where it is important if a reserve is a source or a sink.

This migration effect on the distribution of moose also impacts on the amount of damaged trees in Area 2 as illustrated in Figure 5. Here we can see that the stock of damaged pine is much lower when moose take the risk from hunting into account. Thus, a given hunting effort to protect young pine is more efficient when animals consider hunting risk than in the standard density-dependent framework.

[Figure 5 about here]

### **2.3. Some Empirical Evidence**

Empirically testing for the hypothesis that animals take the risk of predation into account is a non-trivial task. However, an observed change in foraging behavior in North Pacific killer whales provides a suitable natural experiment. Due to the depletion of their usual food, killer whales in this area started to prey on the otter population, Estes et al (1998). This shift in predation patterns started in the early 1990s. Otters are an inferior food for a killer whale, and

represent a diet of last resort. The impact on otter populations has been dramatic. However, one particular area, Clam Lagoon on Adak Island in the Aleutians, is closed to killer whales by natural barriers. Therefore, otters in this lagoon are sheltered from predation. Now if otters are insensitive to predation risk, then Clam Lagoon should act as a source of otters for the surrounding areas by otters migrating to take advantage of the improved opportunities for kelp foraging resulting from killer whales reducing the surrounding otter population. If otters are instead sensitive to predation risk, the Clam Lagoon otter population should, in the steady state, be constant as the result of this shift. In their study, Estes et al (1998) found that the Clam Lagoon otter population remained roughly constant, thus supporting the hypothesis that animals take the risk of predation into account. This is in line with the model presented here.

### **3. Endogenizing human behavior**

So far, we have considered the case where the harvesting of moose is fixed without regard to the observed stocks. Although this may be an appropriate for some regulatory regimes, it is more satisfying to examine the case where human predatory behavior is endogenous. Assume that  $n$  hunters have unrestricted access to Area 2 and that each hunter maximize their instantaneous utility. Hunters are assumed symmetric. This assumption is typical in resource economics and is mathematically one of the simpler cases to handle.<sup>9</sup> Each hunter  $i$  chooses an

effort  $e_i$ . Let the cost effort be  $\frac{c}{2}e_i^2$ . Assume that the productivity of the total hunting effort in Area 2 is proportional to the stock of moose in that area we can write the total catch as:

$$h = qx_2 \sum_{i=1}^n e_i \quad (14)$$

Here  $q$  is the ‘catchability’ coefficient. Let  $\pi$  be the value of harvesting one unit of moose. Hunters are assumed to maximize  $\Pi = \pi h/n - \frac{c}{2}e_i^2 = pqx_2e_i - \frac{c}{2}e_i^2$ . The individual hunting effort is then given by:

$$e_i = \frac{\pi qx_2}{c} \quad (15)$$

Inserting (15) into (14) and normalizing  $n$  to 1 gives the total catch.

$$h = \frac{\pi (qx_2)^2}{c} \quad (16)$$

Inserting (16) into (2) gives the modified equations for the population dynamics.

$$\dot{x}_1 = rx_1 \left(1 - \frac{x_1}{u}\right) + \Phi, \quad \dot{x}_2 = rx_2 \left(1 - \frac{x_2}{u}\right) - \Phi - \frac{\pi (qx_2)^2}{c} \quad (17)$$

To examine the effect of risk sensitivity Equation (13) is modified into:

$$\Phi = \phi \left( \frac{K}{x_1} - \left( 1 - \chi \frac{h}{x_2} \right) \frac{u}{x_2} \right) \quad (18)$$

The parameter  $\chi$  represents a simple way to parameterize the sensitivity of moose to risk.<sup>10</sup>  $\chi = 0$  corresponds to purely density-dependent migratory decisions.  $\chi = 1$  is equivalent to maximizing the expected energy intake when the risk of being killed by hunting is fully accounted for. The dynamics of the system in the absence of hunting is as depicted in Figure 1, with all variables approaching a steady state close to 10.4. The system is assumed to start at a point where all variables take the value of 10. The trajectories are plotted in Figure 6. The first thing to notice from Figure 6 is that as the risk sensitivity  $\chi$  is reduced from 1 to 0, the stock of moose in Area 2 is reduced. Thus, endogenizing human behavior does not affect the conclusions from the previous section. However, from Figure 6 it appears that the moose stock is not an unambiguously decreasing function of  $\chi$ . As  $\chi$  goes from 1/3 to zero, the steady state stock of moose actually falls.

[Figure 6 about here]

Although this may seem paradoxical, the explanation is that when moose migrate purely based on the availability of food in Area 2, the stock of moose in Area 1 becomes so low that the growth rate actually falls through the low stock size. That is, animals migrate out of Area 1 so fast that reproduction declines. Roughly speaking, the mathematical reason is that with a logistic growth function, the maximum growth rate occurs when  $x_1 = K/2$ . When migratory behaviour drives  $x_1$  to a level lower than  $K/2$ , the growth rate falls alongside the stock of  $x_1$ . This is confirmed in Figure 7 where the stock of moose in Area 1 is shown. In the present model  $K = 10$ , so the maximum growth occurs at 5, whereas the steady state level of  $x_1$  is below 2. Therefore, the rate of increase in  $x_1$  is low relative to its potential. The initial response to hunting for all values of  $\chi > 0$  is an increase in the stocks in Area 1 as animals in Area 2 respond to hunting by migrating. As expected, the more risk-sensitive the moose are, the fewer will migrate to Area 2 to exploit the foraging opportunities created by hunting. As in the case with exogenous hunting and risk sensitive animals, the case where  $\chi = 1$  leads to a long-run steady state where the moose stock in Area 1 is roughly equal to the steady state stock in the absence of hunting. Thus, in the steady state moose stocks in Area 1 are unaffected by hunting activity in Area 2.

[Figure 7 about here]

## **4. Summary**

The extent to which animals make rational decisions about migrating behavior has important implications for resource management. If animals only consider foraging opportunities, protecting areas from unwanted wildlife is harder than if animals respond to changes in expected utility. This is illustrated in a model where moose may migrate to areas where they forage on economically valuable young pine trees, but should also have consequences for the ongoing process where wildlife seek shelter in human residential areas. While the importance of animal rationality in a moose/pine model is established, the topic may also be of some interest in other cases. For example, the Norwegian government has decided to set aside some areas as wolf habitats and allow hunting in other areas. The success of this policy depends on whether wolves will learn to stay within the area prescribed or migrate to other areas and forage on farm animals. The results in this paper suggest that economic modeling of such a policy should incorporate the appropriate modeling of wolf behavior. The recommendation is, wherever relevant, that resource economists should consider biological models of animal behavior and incorporate these into management models.

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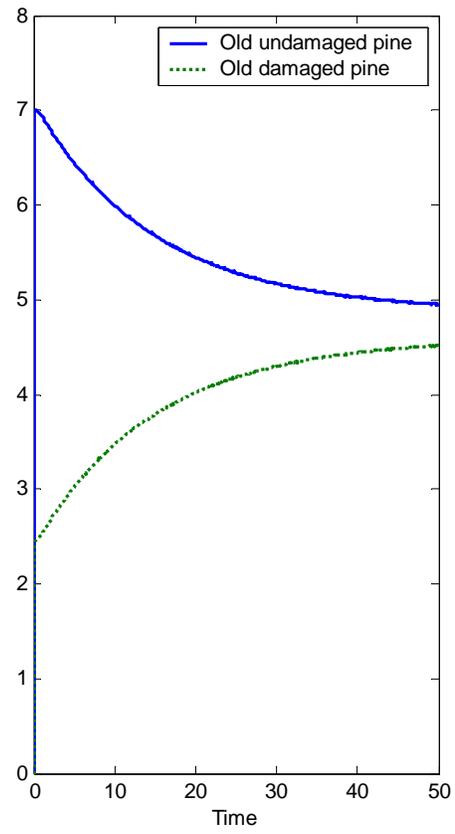
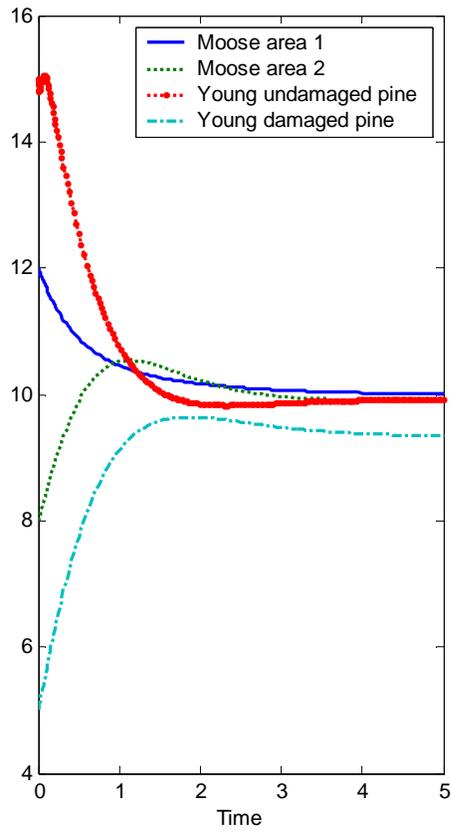
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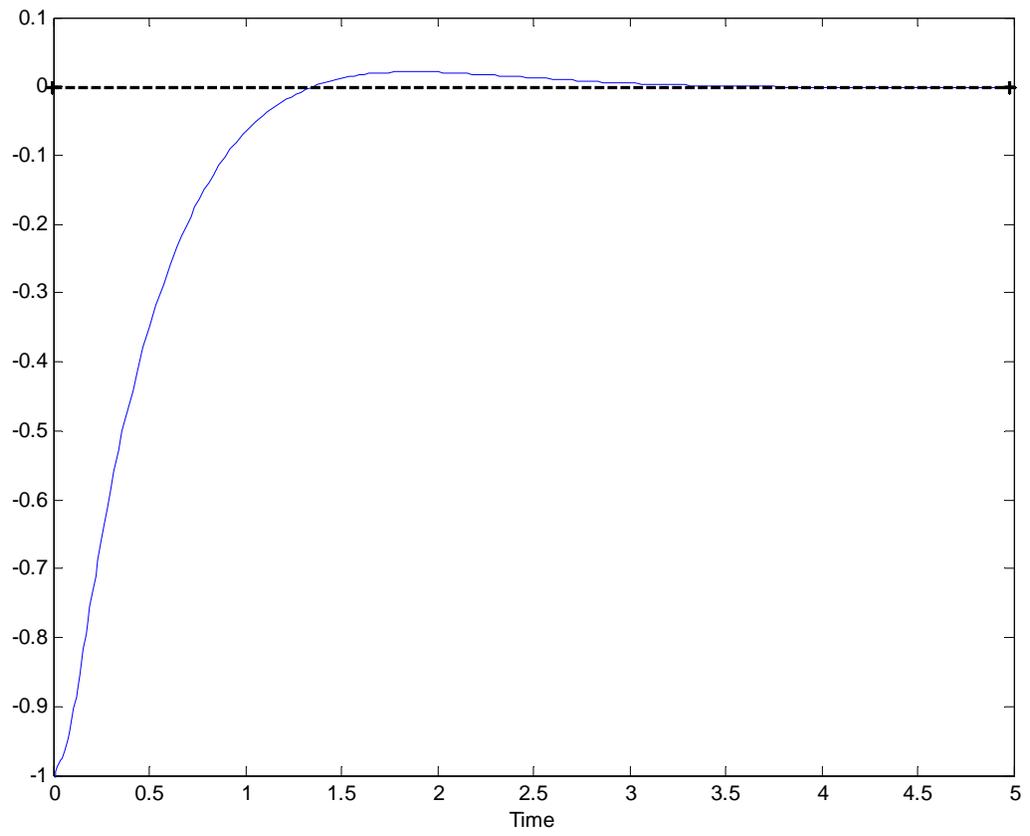
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**Figure 1**



**Figure 2**

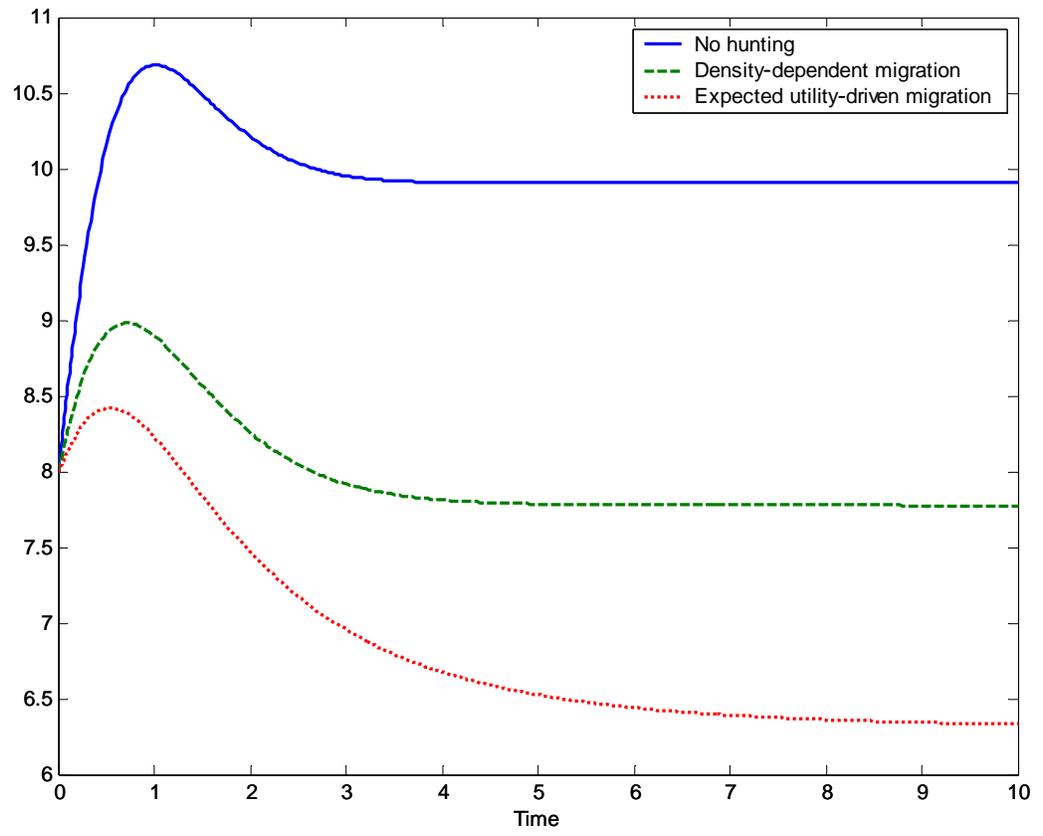


Figure 3

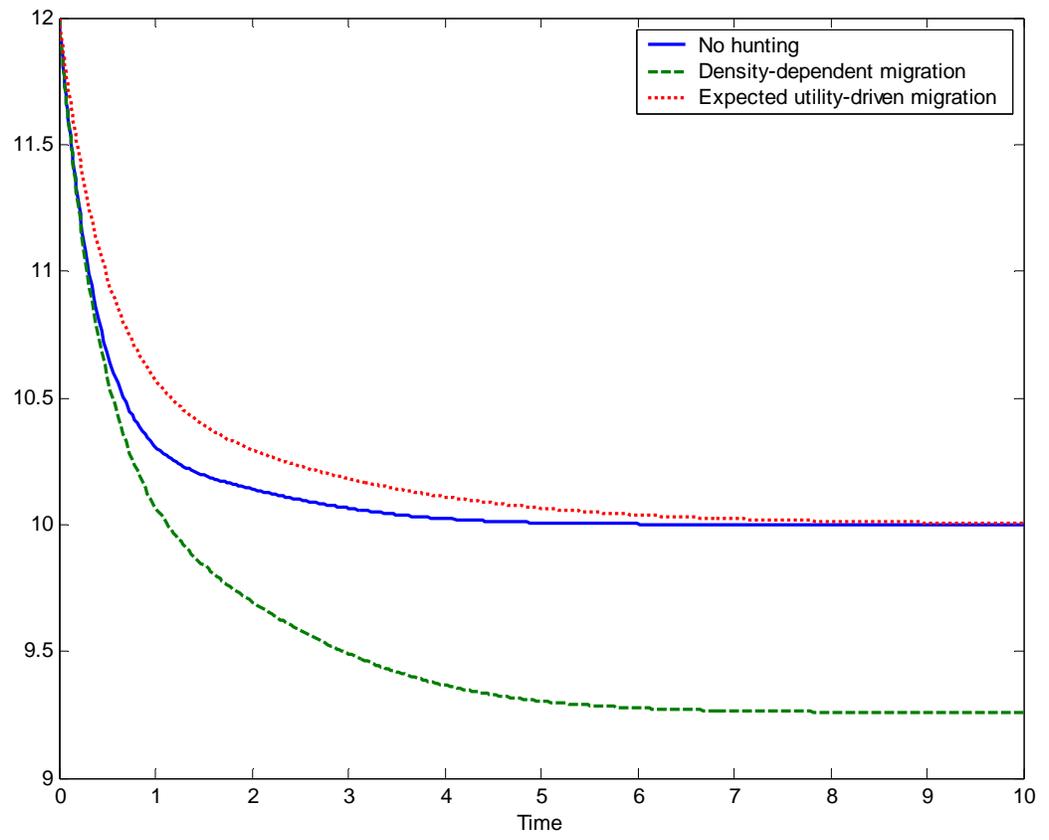


Figure 4

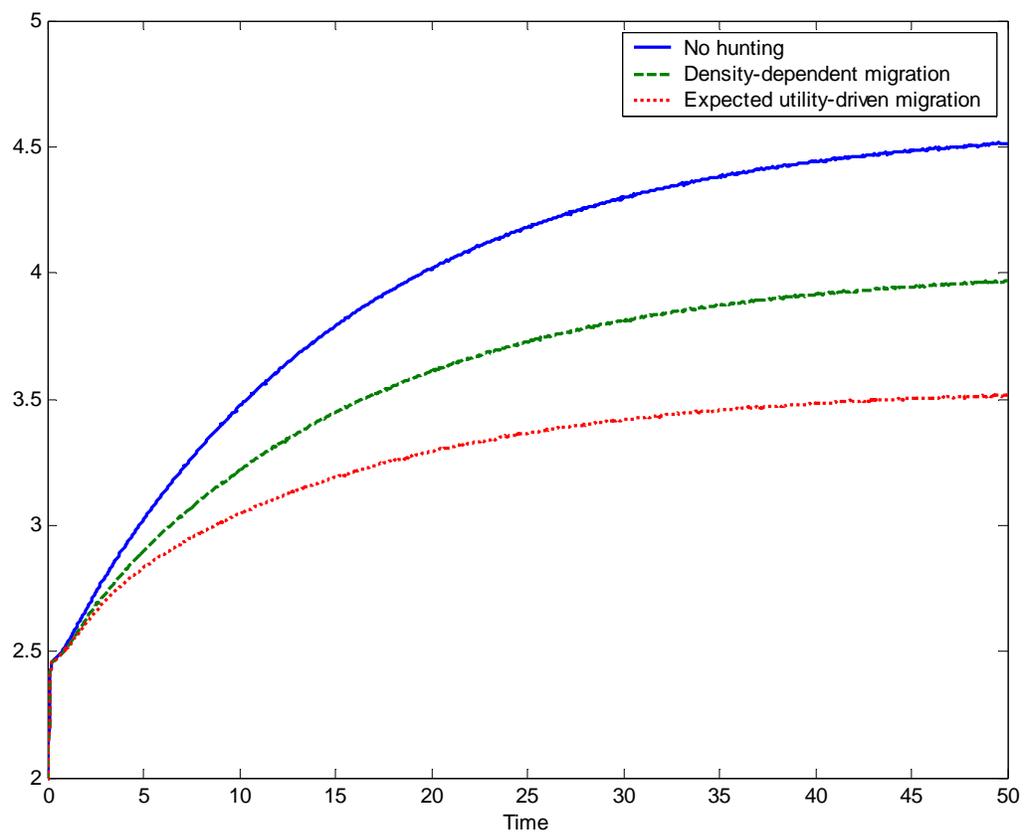


Figure 5

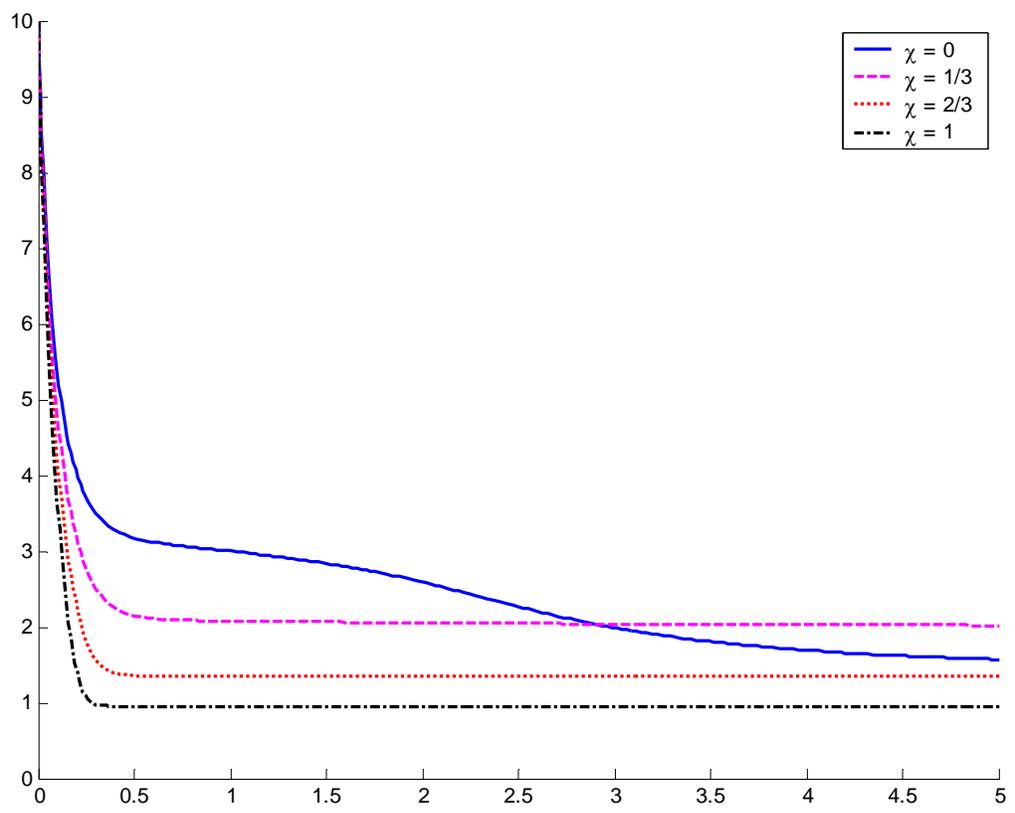


Figure 6

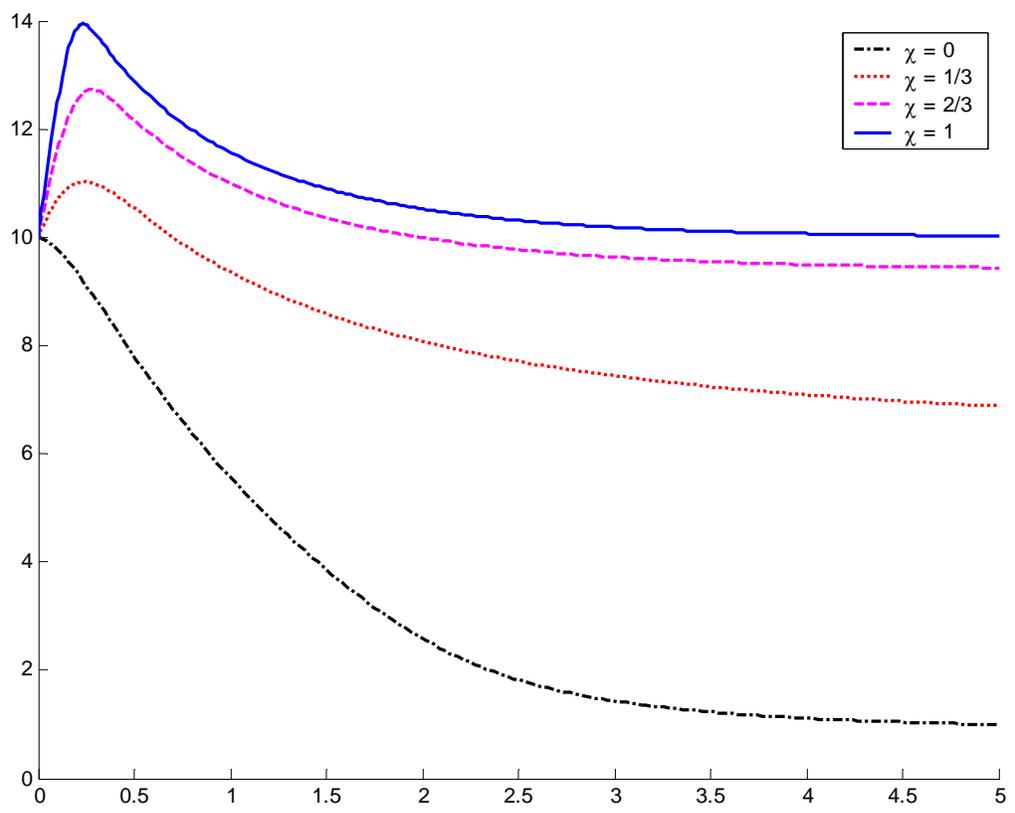


Figure 7

## Figure Captions

***Figure 1.*** The dynamics of equations (1) – (6) with no hunting. Note the difference in time scale. The stocks of animals and young pines converge to the steady state in 5 years. The stock of mature trees converges in 50 years.

***Figure 2.*** Net migration of moose to Area 2 when there is no hunting as a function of time.

***Figure 3.*** Moose stock in Area 2 with hunting as a function of time.

***Figure 4.*** Stock of moose in Area 1 as a function of time.

***Figure 5.*** The effect of hunting on the stock of damaged pine as a function of time.

***Figure 6.*** Stocks of moose in Area 2 as a function of time for various values of  $\chi$ .

***Figure 7.*** Stock of moose in Area 1 as a function of time for various values of  $\chi$ .

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<sup>1</sup> I avoid using the term bioeconomics as a synonym for EMLO as bioeconomics encompasses much more than just resource management issues, Landa & Ghiselin (1999). Of course, resource economics also deals with non-living resources such as oil and solar energy. I know of no term that is specific to the intersection of resource economics and bioeconomics.

<sup>2</sup> Indeed, there is nothing in evolutionary biology that prescribes that rationality, in an evolutionary sense, is limited to the animal world.

<sup>3</sup> These models can sometimes be derived from models incorporating optimizing behaviour and thereby be given what economists would call proper microeconomic foundations, see Pethig & Tschirhart (2001) and Eichner & Pethig (2006).

<sup>4</sup> The term rationality is used in its economic sense, i.e. as an equivalent to optimizing behaviour, although one should recognize that this term may be an inappropriate terminology to employ in other fields where animal behaviour is studied.

<sup>5</sup> Terms like ‘learning’ and ‘conscious decision making’ have strong anthropomorphic connotations and are only used as approximations. It should, however, be noted that some scholars on animal behaviour are willing to accept anthropomorphic terms as an aid to understanding animal behaviour. Indeed, Frans de Waal (1999), a distinguished expert on the behaviour of primates, suggest that ‘anthropodenial’ has harmed the ability to understand some animals.

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<sup>6</sup> Morphological adaptation may come about through genetic selection and/or phenotypic plasticity where a genotype exhibits flexible morphological development in response to environmental conditions.

<sup>7</sup> An additional difference is that the model in Wam et al (2005) model is in discrete time.

<sup>8</sup> Steady-state solutions with pure density-dependent migratory behaviour may be easily found. However, the risk-averse case requires the solution of quartic non-additive equations. Numeric analysis is employed as a simpler alternative.

<sup>9</sup> We do not consider the optimal management of these areas in this analysis. This problem is technically quite involved and requires characterizing solutions that consider multiple dynamic equilibria. The thorough analysis of these issues would require further work.

<sup>10</sup> This measure of risk sensitivity must not be confused with measures of risk averseness. This is because risk sensitivity is intended to measure the awareness of risk, rather than the attitude towards risk.