

**Managing Genetic Resources for Fun and Profit**  
**– The Role of the Interest Rate in Natural Selection**

By

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# **Managing Genetic Resources for Fun and Profit**

## **– The Role of the Interest Rate in Natural Selection**

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Atle G. Guttormsen, Dadi Kristofersson and Eric Nævdal\*

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### **Abstract**

It has become clear that exploitation of natural resources may result in evolutionary selection pressure resulting in morphological changes of a species over time. This potentially adverse effect should be taken into account when regulating the use of such resources. In this paper we present a bioeconomic model where we analyse the effect of selective harvesting on genetic frequency for one specific gene in terms of the socially optimal long-term management of the resource. It is assumed that the individuals carrying the gene have a lower natural mortality rate but are also more valuable to catch. Results indicate that the relationship between the natural rate of selection against less valuable individuals and the interest rate is crucial in determining whether the valuable gene should be preserved or allowed to become extinct. To our knowledge this is the first economic model of resource harvesting when harvesting directly affects the rate of selection in a genetic model.

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## Introduction

The principles of modern management of renewable resources were to a large extent developed during the 1950s when intellectual threads from biology and economics emerged and formed a rationale for renewable resource management, (Wilen 1999).<sup>1</sup> Since then resource economists have relatively closely followed the development in the biological and ecological sciences, and included new wisdom from these research areas into the bioeconomic models underlying most of the literature on resource management.

However it appears that economists to some degree have missed one strand of the ecological and biological literature. At least since the 1970s biologist have been aware of the possibility that selective harvesting or hunting could alter the genetic pattern of a resource, Heino (1998). Since then, man-made selection pressure on wild stocks has been a debated issue in the biological and ecological literature. Resource economists on the other hand have only to a limited extent shown interest in the management of renewable resources where exploitation potentially leads to malign genetic selection. Biologists have long been aware that human exploitation of reproducing natural resources may affect these resources on a genetic level. Whenever a resource is harvested in a way that is not completely random, genetic selection will take place to some degree. Two cases have received considerable attention in the ecological literature. Hunters often look for specific physiological traits, such as body size or antler size, in their prey, Harris *et al* (2002). In fisheries, harvesting technology consistently favors individuals of small size. However, any human influence on an ecosystem that

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<sup>1</sup> Wilen (2000) especially mention the articles by Beverton and Holt (1957) and Schaefer, (1957) from biology and from Gordon (1954) and Scott (1955) in economics.

consistently and significantly favors or selects against particular genetic traits in a species, will affect the genetic distribution of that species. Possibly, due to ecological feedbacks, the distribution of genes may be affected within the entire ecosystem.

There is a large ecological literature showing both theoretically and empirically that confirms that human harvesting affects the distribution of genes in ecosystems. Thelen (1991), Jorgenson *et al* (1993), Reznick, Bryga and Endler (1990), Coltman *et. al* (2003) all examine the effect of hunting on various ungulates, Tenhumberg *et. al* (2003) discuss how kangaroos are affected by selective harvesting in Australia, whereas Law (2000), Heino and Godø (2002), and Conover and Munch, (2003) among several others examine fisheries. Ecologists have recently started to examine the implications of selective harvesting for resource management (Heino, 1998). However, ecologists use their own notions of objectives for resource management as Maximum Sustainable Yield seems to be the objective of choice, Heino (1998). This concept is of course fundamentally flawed as a resource management objective, Samuelson (1976).

A rationale for the interest by economist of biodiversity came with the Rio Declaration on Biological Diversity. The convention was concluded in the UN Conference on Environment and Development in Rio in 1992. Subsequently it has been signed by the requisite number of nations and has now come into effect. In the declaration biodiversity is defined as “The variability among living organisms from all sources including, *inter alia* terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are a part; this includes diversity within species and of ecosystems”. In this view genetic diversity is in itself a good reason to attach value to the existence of genetic variation. This is the perspective taken in most of the economic literature where various measures of biodiversity assign benefits to genetic variation, Weitzman (1992), Weitzman

(1993), how to value these benefits and how to regulate ecosystems with diversity measures as policy objectives. Polasky *et al* (1993), Polasky and Solow (1995). As pointed out by Xepapadeas and Broch (2003), (XB), the value assigned value to biodiversity or genetic diversity is usually a measure of diversity per se and not linked to the value of specific genes as inputs to human production of goods and services. To our knowledge XB is the only exception. XB examines a model where the various plants vary in their resistance to insect pests. The genetic model in XB is assumed described by a Hardy-Weinberg equilibrium. A Hardy-Weinberg equilibrium, sometimes referred to as a law, is characterised by the distribution of genotype frequencies being constant from generation to generation. The Hardy-Weinberg equilibrium applies to large populations with random mating. Crucially, this equilibrium assumes that there are no selection effects.

However based on the knowledge that human harvesting affects the distribution of genes, we will utilize a genetic model were the Hardy-Weinberg equilibrium does not apply, except in steady state. The difference lays in that in our model resource harvesting affects the *rate* at which natural selection occurs. The difference between the genetic components in XB and our study may be summed up as XB employing a model with slow population dynamics and rapid genetics whereas in our model population dynamics are rapid and genetics are slow. The appropriateness of the different approaches depends on the relationship between biomass growth and the length of the reproductive cycle, with our model being more appropriate for resources with relatively long reproductive cycles. This would be the case with e.g. mammals and large fish.

We will use the genetic model to further construct a bioeconomic model where we analyze the effect of selective harvesting on genetic frequency for one specific gene in terms of the socially optimal long-term management of the resource. This

objective is determined solely through the profits generated by harvesting. We do not specify why harvesting is selective, but take this as given.

## A Model with Population and Genetic Dynamics.

### Population dynamics

Consider a population with two phenotypes, labeled “bad” ( $B$ ) and “good” ( $G$ ). The biomass of each phenotype at any given time is given by  $x_i$ ,  $i = G, B$ . Total biomass is given by  $x = x_G + x_B$ . The population dynamics of each phenotype is assumed driven by the following differential equations:

$$\dot{x}_i = r_i x_i \left( 1 - \frac{x_G + x_B}{K} \right) - \delta_i x_i - h_i, \quad i = G, B. \quad (1)$$

Here  $r_i$  is growth rate,  $\delta_i$  are mortality rate and both are positive parameters,  $K$  is the carrying capacity and  $h_i$  is harvesting of biomass belonging to phenotype  $i$ . The total change in biomass is given by  $\dot{x} = \dot{x}_G + \dot{x}_B$ . We want to consider the regulation of the population when different phenotypes have different biological productivity. It is assumed that phenotype  $B$  is biologically less productive than phenotype  $G$ . We model this by assuming that that  $r_B = r_G = r$  and  $\delta_G < \delta_B < r$ . The expression  $r - \delta_B$  is the intrinsic growth rate of phenotype  $B$ , and will be important in the sequel. It is further assumed that the number of individuals is equally proportional to the biomass for both phenotypes and the proportion is arbitrarily set to one. This implies that the number of individuals of each phenotype is equal to the biomass. An expression that is of importance below is the *coefficient of selection*,  $s$ . This coefficient gives the relative fitness of one phenotype relative to another, i.e., a measure of the extent to which natural selection is acting to reduce the relative contribution of a given genotype to the next generation.  $s$  is here given by:

$$s = \frac{\dot{x}_G}{x_G} - \frac{\dot{x}_B}{x_B} = -(\delta_G - \delta_B) - \frac{h_G}{x_G} + \frac{h_B}{x_B} \quad (2)$$

In the absence of harvesting,  $s = s^* = \delta_B - \delta_G > 0$  indicating that  $G$  is selected for.  $s^*$  is the intrinsic coefficient of selection. It can be shown that in the absence of harvesting there is only one stable biological equilibrium given by  $x_B = 0$  and  $x_G = K(1 - \delta_G/r)$ . However, if harvesting effort directed at phenotype  $G$  is sufficiently large relative to harvesting effort directed at phenotype  $B$ , then  $s$  changes sign and  $G$  is selected against, leading to reduction in the  $x_G$  stock and even the extinction of phenotype  $G$ . There is therefore a risk that genetic resources will be mismanaged if not properly considered in management strategies. It is this possibility that is the main motivation for this paper.

## Genetic Dynamics

The determination of phenotypes is determined by the gene frequency.<sup>2</sup> Here a standard model of Mendelian genetics is assumed. There are two alleles,  $A$  and  $a$ , of the same gene. Thus there are two possible homozygotes,  $AA$  and  $aa$ , and one heterozygote  $Aa$ . When relating the genotype to the phenotype, a large number of variations are possible. Here it is assumed that individuals of genotype  $AA$  and  $Aa$  are of phenotype  $G$  and individuals of genotype  $aa$  are  $B$ . Let the frequency of  $a$  be  $q$ . Under the assumption that mating between genotypes is non-preferential and well mixed, the frequency of  $AA$  is  $(1 - q)^2$ , the frequency of  $Aa$  is  $2q(1 - q)$  and the frequency of  $aa$  is  $q^2$ . the fraction of  $x$  that is  $x_G$  is hence  $(1 - q)^2 + 2q(1$

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<sup>2</sup> There is an important issue that is suppressed here. Here all of the phenotypic variation is prescribed to genetic variation. In the real world, part of the morphologic variation in a given species size is due to phenotypic plasticity. This is the morphological variation that is possible within a single genetic variety. This plasticity is caused by environmental factors. The frequency of different phenotypes may in itself be on such environmental factor.

$-q) = 1 - q^2$ . It follows that  $x_G = (1 - q^2)x$  and  $x_B = q^2x$ . We further assume that only the individuals of type  $G$  are of commercial interest, and that harvesting is totally selective such that no harvesting of type  $B$  occurs. The changes in  $x$  are therefore determined by the following differential equation:

$$\dot{x} = rx \left(1 - \frac{x}{K}\right) - \delta_G (1 - q^2)x - \delta_B q^2 x - h_G \quad (3)$$

Because of the evolutionary pressure imposed by selection, the Hardy-Weinberg law may not apply and  $q$  will be a non-constant function of time. It can be shown that  $q$  is determined by the following differential equation:<sup>3</sup>

$$\dot{q} = -\frac{sq^2(1-q)}{1-sq^2} \quad (4)$$

Here  $s$  is given by Equation (2). From Equation (4) it is obvious that if  $s$  is a constant not equal to zero, then there are only two steady states,  $q = 0$  and  $q = 1$ . If  $B$  is selected against, then  $s$  is positive and  $q$  approaches zero for any initial value of  $q$ . This will for instance be the case in the absence of harvesting when  $s = -(\delta_B - \delta_G) > 0$ . If  $s$  is negative, then  $G$  is selected against and  $q$  converges to 1.

## Optimal Management

The following analysis will focus on how selection affects the dynamics of  $q$ . For most species, genetic dynamics are relatively slow compared to population dynamics. It is therefore assumed that the population at every point in time is at a population dynamic equilibrium determined by  $\dot{x} = 0$ . By solving (3) with respect to  $h_G$  the following relationship between  $x$  and  $h_G$  is found

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<sup>3</sup> This is a basic result in quantitative genetics. See e.g. Falconer and Mackey (1996) for an exposition.

$$h_G = rx \left(1 - \frac{x}{K}\right) - \delta_G (1 - q^2)x - \delta_B q^2 x \quad (5)$$

It assumed that the harvesting depends on harvesting effort,  $E$  such that:

$$h_G = \gamma x_G E = \gamma (1 - q^2) x E \quad (6)$$

where  $\gamma$  is the catchability coefficient. Inserting this expression into Equation (5) and solving for  $x$  gives:

$$x = \frac{K}{r} (r - \delta_G - \gamma E) + \frac{q^2 K}{r} (\delta_G - \delta_B + \gamma E) \quad (7)$$

Instantaneous harvesting is then given by

$$h_G = \frac{\gamma (1 - q^2) K}{r} \left( (r - \delta_G - \gamma E) + q^2 (\delta_G - \delta_B + \gamma E) \right) E \quad (8)$$

Further, it follows from (6) and (2) that the coefficient of selection,  $s$ , is given by:

$$s = \delta_B - \delta_G - \gamma E \quad (9)$$

To examine the optimal regulation of the natural resource, it is assumed that a regulator wants to maximize the discounted profits from harvesting the resource. Harvesting is assumed to be costless and valued at an exogenous price  $p$ . The objective function is then:

$$\begin{aligned} \max_E \left( \int_0^\infty p h_G e^{-\rho t} dt \right) = \\ \max_E \left( \int_0^\infty p \left( \frac{\gamma (1 - q^2) K}{r} \left( (r - \delta_G - \gamma E) - q^2 (\delta_B - \delta_G - \gamma E) \right) E \right) e^{-\rho t} dt \right) \end{aligned} \quad (10)$$

where  $\rho$  is the discount rate. The maximisation in Equation (10) is performed subject to:

$$\dot{q} = -\frac{q^2(1-q)(\delta_B - \delta_G - \gamma E)}{1 - (\delta_B - \delta_G - \gamma E)q^2} \quad (11)$$

The Hamiltonian for this problem is given by:

$$H = \frac{p\gamma(1-q^2)K}{r} \left( (r - \delta_G - \gamma E) - q^2(\delta_B - \delta_G - \gamma E) \right) E + \lambda \left( -\frac{q^2(1-q)(\delta_B - \delta_G - \gamma E)}{1 - (\delta_B - \delta_G - \gamma E)q^2} \right) \quad (12)$$

In addition to the relevant transversality conditions, necessary conditions for an optimal program are given by Equation (11) and:<sup>4</sup>

$$\frac{\partial H}{\partial E} = \frac{p\gamma K(1-q^2)}{r} \left( (r - \delta_G - 2\gamma E) - q^2(\delta_B - \delta_G - 2\gamma E) \right) + \frac{\lambda\gamma(1-q)q^2}{(1 - q^2(\delta_B - \delta_G - \gamma E))^2} = 0 \quad (13)$$

$$\dot{\lambda} = \rho\lambda + \frac{2\gamma pqKE}{r} \left( (r - \delta_G - \gamma E) + (1 - q^2)(\delta_B - \delta_G - \gamma E) \right) + \lambda q(\delta_B - \delta_G - \gamma E) \frac{(q^3(\delta_B - \delta_G - \gamma E) - 3q + 2)}{(1 - q^2(\delta_B - \delta_G - \gamma E))^2} \quad (14)$$

The complexity of the condition in (13) and (14) give little hope of finding an explicit solution that fully characterizes the problem. Further, isolating  $E$  in Equation (13) involves solving a cubic polynomial. However, Equation (11) has a structure that enables us to find steady states with relative ease. From Equation (11) it is evident that there are three conditions under which  $\dot{q} = 0$ .  $q = 0$ ,  $q = 1$

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<sup>4</sup> By calculating the second derivative with respect to  $E$  one can show that the Hamiltonian is not necessarily concave with respect to  $E$ . In this case, setting  $E = 0$  will maximize the Hamiltonian. This is not further discussed.

and  $s = \delta_B - \delta_G - \gamma E = 0$ . The two first cases correspond to either of the genes not being present in the population. The case  $\delta_B - \delta_G - \gamma E = 0$  is the most interesting as both genes are present in the population. Note that in steady state, evolution does not select for any of the genes.

The steady state value of  $\lambda$  when  $s = 0$  is given by:

$$\lambda = -\frac{2pqK}{r\rho}(r - \delta_B)(\delta_B - \delta_G) \quad (15)$$

The negativity of  $\lambda$  is an obvious implication of  $B$  being unwanted. Inserting this value of  $\lambda$  and  $s = 0$  into (13) gives a fourth order polynomial equation for determining steady state value of  $q$ .

$$\begin{aligned} \frac{\partial H}{\partial E} = \Theta(q) &= \frac{\gamma K p}{r} [a_0 + a_1 q + a_2 q^2 + a_3 q^3 + a_4 q^4] = 0 \\ &= \frac{\gamma K p}{r} \left[ (r - \delta_B)(1 - q^2) - (\delta_B - \delta_G)(1 - q^2)^2 - \frac{1}{\rho}(r - \delta_B)(\delta_B - \delta_G)(2(1 - q)q)q^2 \right] \end{aligned} \quad (16)$$

Here  $a_0 = r + \delta_G - 2\delta_B$ ,  $a_1 = 0$ ,  $a_2 = -(r + 2\delta_G - 3\delta_B)$ ,  $a_3 = -\frac{2}{\rho}(r - \delta_B)(\delta_B - \delta_G)$  and  $a_4 = \frac{1}{\rho}(2r - 2\delta_B - \rho)(\delta_B - \delta_G)$ . The expression  $\Theta(q)$  is key to determining not only the steady state values of  $q$ , but also the stability properties of these steady states. A fourth order polynomial may have at most four real roots. The sign of  $a_3$  is negative given the assumptions of the model. The signs of the other parameters are determined by the values of  $r$ ,  $\delta_G$ ,  $\delta_B$  and  $\rho$ . The root  $q=1$  can be determined from the expression (15) and since  $a_1=0$  then  $q=0$  is a solution to  $\partial\Theta(q)/\partial q = 0$  so there must be at least one root in  $q < 0$ . There are therefore two roots that can potentially be found in  $[0, 1)$ . The following expressions are important in determining the number of roots in  $[0, 1)$ .

$$\Theta(0) = \frac{\gamma K p}{r} a_0 = \frac{\gamma K p}{r} (r - \delta_B - (\delta_B - \delta_G)) \quad \Theta'(1) = \frac{2\gamma K p}{r\rho} (r - \delta_B)(\delta_B - \delta_G - \rho) \quad (17)$$

If  $\Theta(0) > 0$  and  $\Theta'(1) > 0$  there can be only one root in  $[0, 1)$ . Similarly, if  $\Theta(0) < 0$  and  $\Theta'(1) < 0$  there can be only one root in  $[0, 1)$ . Further, since the sign of  $a_3$  is negative by assumption there cannot exist a root in  $[0, 1)$  for  $\Theta(0) > 0$  and  $\Theta'(1) < 0$ . For the last case,  $\Theta(0) > 0$  and  $\Theta'(1) < 0$ , there can either exist no or two roots depending on the parameter values of expression (16). We can therefore limit our discussion to these five cases.

Before we begin, let us consider the interpretation of the three key expressions that make up Equation (16). First, the expression  $(r - \delta_B)$  gives the intrinsic productivity of phenotype  $B$ . It measures how fast phenotype  $B$  regenerates. This is of interest since the heterozygotes are of phenotype  $G$  and the more productive phenotype  $B$  is the more it contributes to the growth of the commercially interesting heterozygotes. Second, the expression  $(\delta_B - \delta_G)$  gives the selection in absence of harvesting or the rate at which nature selects for phenotype  $G$ . This can also be interpreted as the internal rate of return on preserving phenotype  $G$ , since only phenotype  $G$  is of value and the stock size is in steady state. The third part is simply the discount rate  $\rho$ , which measures the alternative value of capital to the returns on alternative investments

**Case 1,**  $\Theta(0) > 0$  and  $\Theta'(1) > 0$ , corresponding to  $r - \delta_B > \delta_B - \delta_G$  and  $\delta_B - \delta_G > \rho$ . This implies that phenotype  $B$  has higher intrinsic productivity than the internal rate of return on preserving phenotype  $G$ , which again indicates that some positive value of  $q$  is optimal. However, the internal rate of return is greater than the alternative value of capital, given by the discount rate, which indicates that extinction of the  $G$  type cannot be optimal.  $\Theta(0) > 0$  and  $\Theta'(1) > 0$  indicate one, and only one, root to  $\Theta(q) = 0$  in the interval  $(0, 1)$ , since the maximum number of roots is two. The shape of  $\Theta(q)$  is illustrated in Figure 1. There are two steady states,  $q = 1$  and  $q = q^*$ , as expected. The stability properties of these steady states are of some interest. Here we use a heuristic method based on the fact that  $\Theta(q)$  is the instantaneous marginal benefit of  $E$ , evaluated for the steady state value of  $E$ , given  $q$ . This implies that close to the steady state values of  $q$ ,  $\Theta(q)$  is close to the marginal benefit of an increment in

$E$  relative to the steady state value. Thus for a value of  $q$  slightly smaller than  $q^*$ ,  $\Theta(q) > 0$  so it pays to increase  $E$  relative to the steady state value of  $E$ . Because of the particular shape of  $\dot{q}$ , this implies that  $q$  will increase and move towards  $q^*$ . For values of  $q$  slightly larger than  $q^*$ ,  $\Theta(q) < 0$  so it pays to decrease  $E$  slightly relative to the steady state value of  $E$ .  $\dot{q}$  will then be negative and move towards  $q^*$ . It follows that  $q^*$  is a stable steady state.

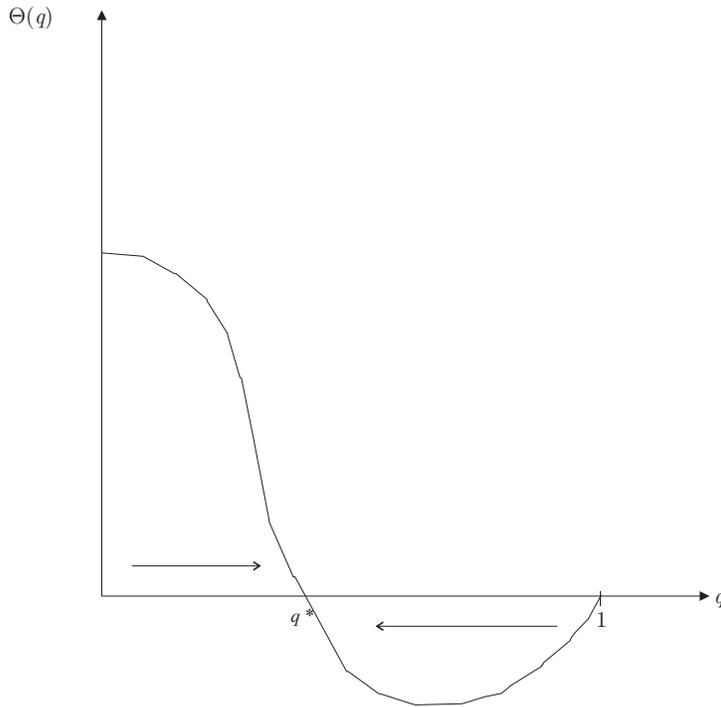


Figure 1,  $\Theta(q)$  for Case 1.

By the same reasoning,  $q = 1$  is unstable. If  $q$  is slightly smaller than 1,  $\Theta(q) < 0$  so it pays to decrease  $E$  relative to the steady state value.  $q$  will then decrease and move away from the steady state. Now  $q = 0$  is not a steady state. The figure therefore fully supports the initial interpretation that some coexistence of the two phenotypes is optimal. As  $\Theta(q)$  is only equal to the true value of the marginal benefit of  $q$  when  $\Theta(q) = 0$ ,  $\Theta(q)$  may be significantly different from the

marginal benefit of  $E$ . However, it can be shown that  $\Theta(0)$  has the same *sign* as the true value of the marginal value of  $E$  evaluated at  $E = 0$ . Therefore, one would want to increase  $E$  relative to the steady state for all  $q < q^*$  and  $q$  will therefore increase until  $q = q^*$ .  $q^*$  is therefore a stable steady state and for any initial value of  $q \in [0, 1)$ , optimal management will converge to this steady state where both genotypes are present in equilibrium. The argument above indicates that the sign of  $\Theta'(q^*)$  determines the stability property of the steady state. This is formally shown in the appendix.

**Case 2.**  $\Theta(0) > 0$  and  $\Theta'(1) < 0$ . This corresponds to  $r - \delta_B > \delta_B - \delta_G$  and  $\delta_B - \delta_G < \rho$ . The first inequality implies that phenotype  $B$  has higher intrinsic productivity than the internal rate of return on preserving phenotype  $G$ . Some  $q > 0$  is therefore optimal. However, the internal rate of return is less than the alternative value of capital indicating that the value of the resource is better managed in alternative investments. The shape of  $\Theta(q)$  is illustrated in Figure 2. Here,  $\Theta(q) > 0$  for all  $q$ . The optimal choice of  $E$  is therefore always higher than the steady state level of  $E$  and  $q \rightarrow 1$  as  $t \rightarrow \infty$ . For this combination of parameter values, it is always optimal to let the gene  $A$  become extinct.

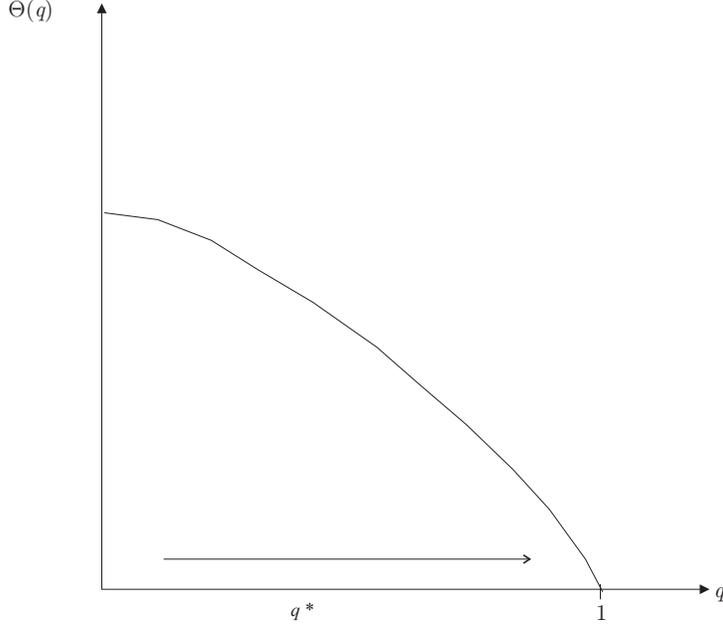
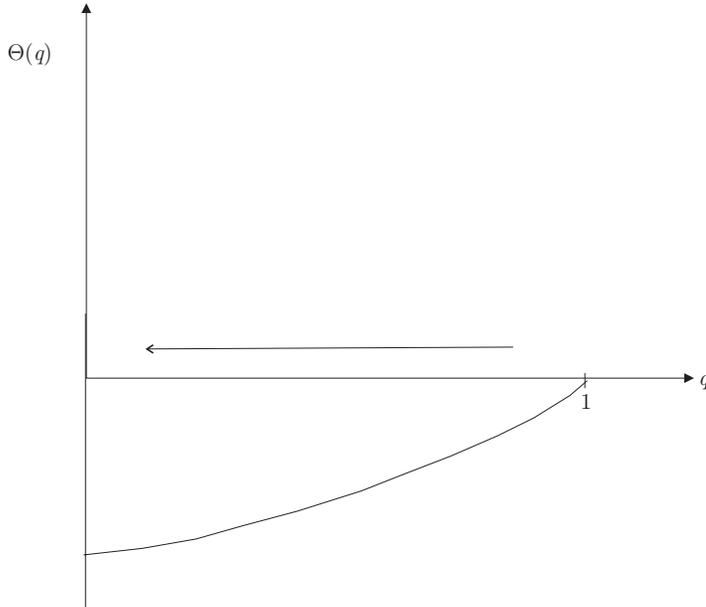


Figure 2,  $\Theta(q)$  for Case 2.

**Case 3**,  $\Theta(0) < 0$  and  $\Theta'(1) > 0$ . This case has two possible solutions, no and two roots in  $[0,1)$ . The first inequality corresponds to  $r - \delta_B < \delta_B - \delta_G$ , which implies that phenotype  $B$  has lower intrinsic productivity than the internal rate of return on preserving phenotype  $G$ , which does not imply that a positive value of  $q$  is optimal. Further,  $\delta_B - \delta_G > \rho$  implies that the internal rate of return is greater than the alternative value of capital, given by the discount rate, which indicates that extinction of type  $G$  cannot be optimal. Let us look at the graphical illustration of each case. Figure 3a shows the case with no roots in  $[0,1)$  where it does not pay to harvest the steady state levels of  $E$  for any value of  $q$ . Here the intrinsic rate of growth for phenotype  $B$  is so low and the internal interest rate so high that phenotype  $B$  never becomes a significant part of the population. This case may be interpreted as the case that gives the same result as

the standard resource management model without selection. However, this requires that optimal  $E$  lies below the  $s^*/\gamma$  for all values of  $q$ .



**Figure 3a,  $\Theta(q)$  for Case 3 with one root.**

On the other hand figure 3b shows the solution with two roots in  $[0,1)$ , e.g. for the parameter values:  $r=0.61$ ,  $\delta_G=0.28$ ,  $\delta_D=0.45$  and  $\rho=0.15$ . In this case it does not pay to harvest the steady state levels of  $E$  for any value of  $q$  below  $q_1$ . However if  $q$ , e.g. by mismanagement, gets pushed to the steady state level  $q_1$  the sign changes and it becomes optimal to increase effort until a new equilibrium is reached at  $q_2$ . The steady state point  $q_1$  is an unstable equilibrium, a Skiba point (Skiba 1978). On the other hand,  $q_2$  is a stable equilibrium since it is optimal to reduce effort for any  $q > q_2$  and optimal management will converge to this steady state where both genotypes are present in equilibrium.

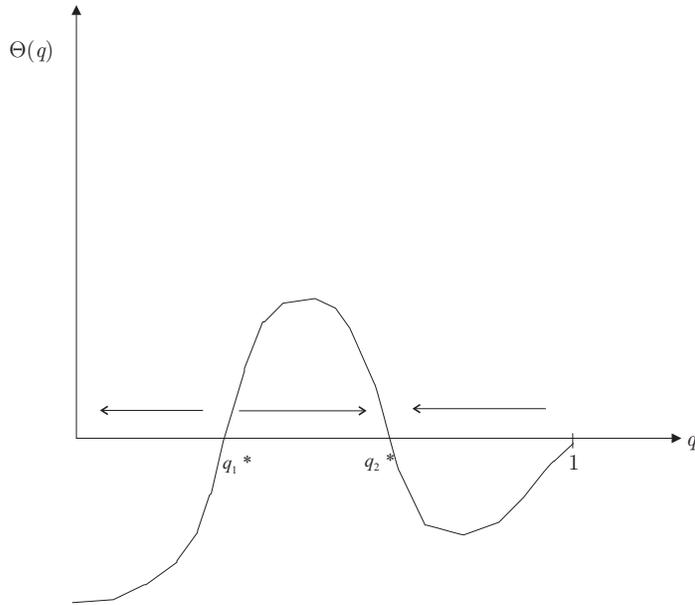
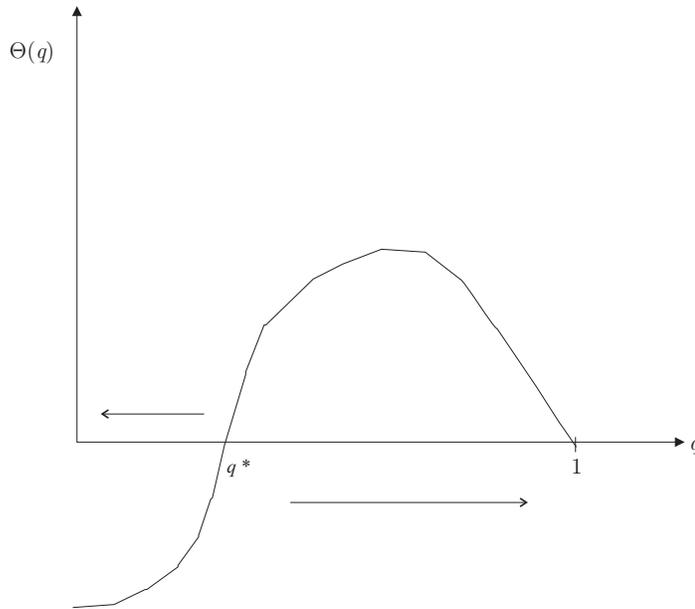


Figure 3b,  $\Theta(q)$  for Case 3 with two roots.

**Case 4.**  $\Theta(0) < 0$  and  $\Theta'(1) < 0$ . which corresponds to  $r - \delta_B < \delta_B - \delta_G$  and  $\delta_B - \delta_G < \rho$ . The first inequality implies that phenotype  $B$  has lower intrinsic productivity than the internal rate of return on preserving phenotype  $G$ , which does not imply that a positive value of  $q$  is optimal. However, the second inequality implies that the internal rate of return is less than the alternative value of capital, which indicates that extinction of phenotype  $G$  can be optimal. This is the most dangerous case in terms of classical management where genetic resources are not taken into account. It is optimal to conserve at low levels of  $q$ , because of the low productivity of phenotype  $B$  but at some point the low internal rate of return makes the extinction of phenotype  $G$  optimal. This case is illustrated in figure 4. It shows a steady state in the interior of  $[0, 1)$ , but this steady state is not stable. Rather, it is a Skiba point, Skiba (1978).



5

**Figure 4,  $\Theta(q)$  for Case 4.**

For low values of  $q$ , it is optimal to set  $E$  below the steady state level and conserve the highest possible fraction of phenotype  $G$ . This raises the question of economic management of resources that have been historically poorly managed. Such poor management may lead to initial values of  $q$ , that may well be larger than  $q^*$ . At this point, the density dependence of biomass growth has rendered phenotype  $G$  relatively unproductive. The cost of restoring phenotype  $G$  is then

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<sup>5</sup> There has recently been an increasing interest in Skiba points in the resource economic literature on non-linear natural resource problems. See e.g. Brock and Starrett (2003) or Crépin (2003). The results presented in these papers are consistent with the conclusions presented here.

too high as it is only weakly selected for in the absence of harvesting. The term weakly selected for is here defined relative to the interest rate.

## Concluding remarks

In this paper we have addressed the optimal management of the genetic resources of a renewable resource. The results presented in this paper suggest an interesting dichotomy between economic and biological factors with clear links to established results in natural resource economics. The model identifies two important determinants of optimal management, one for a small share of the inferior gene and another for a large share. An increase in the frequency of an unwanted gene,  $q$ , is optimal if the intrinsic growth rate of the unwanted phenotype exceeds the internal rate of return in the resource. On the other hand, an increase in  $q$  at a high frequency is optimal if the internal rate of return in the resource exceeds the opportunity cost of capital, measured by the discount rate. We identify five different solutions to the problem. Two solutions are of special interest to current management regimes of natural resources. Both involve low intrinsic growth rates of the inferior phenotype compared to the internal rate of return. We have shown that a Skiba point may exist in such solutions where mismanagement of genetic resources may lead to an increase in the frequency of an inferior gene beyond a point where extinction is the optimal solution.

There are two simplifications in the present model whose inclusion affects the result. First, the productivity and cost of harvesting is not affected by the composition of the stock. It seems reasonable to suspect that this is not the case, e.g. that the lower the frequency of phenotype  $G$  the higher the harvest cost. Second, we assume that only phenotype  $G$  is of commercial value and that no harvest occurs of phenotype  $B$ . This simplification describes trophy hunting fairly well but is a poor description of many renewable natural resources such as fisheries. However, since this problem is a very relevant in fisheries, as technological improvements allow more selective fishing, this assumption should

be challenged. Our results demonstrate that it may be of great importance for the optimal management of natural resources that the management of genes is taken into account

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## Appendix. Formal Proof of the Stability Analysis

In the main text, a sufficiency condition for the stability of a steady state  $q^*$  is that  $\Theta'(q^*) < 0$ . Conversely, a sufficiency condition for instability of  $q^*$  is that  $\Theta'(q^*) > 0$ .  $\Theta'(q)$  is given by  $\left(\frac{\partial H}{\partial q}\right)_{E=\frac{\delta_B - \delta_S}{a}}$ . To prove this consider the following general optimal control problem:

$$\max \int_0^\infty U(q, E) e^{-\rho t} dt \quad s.t. \dot{q} = f(q, E), q(0) \text{ given.}$$

Along the optimal path,  $\dot{q} = f(q, E(q))$ . Here  $E(q)$  is the optimal choice of  $E$  as a function of  $q$ . Denote  $E(q^*)$  as  $E^*$ . In the present problem  $\left(\frac{\partial H}{\partial q}\right)_{E=E^*} = U''_{Eq}(q, E^*) + \lambda f''_{Eq}(q, E^*)$ . Stability of  $q^*$  holds if

$$\left(\frac{\partial \dot{q}}{\partial q}\right)_{q=q^*} = \left(\frac{\partial f}{\partial q}\right)_{q=q^*} + \left(\frac{\partial f}{\partial E}\right)_{q=q^*} \left(\frac{dE}{dq}\right)_{q=q^*} < 0$$

An expression for  $\frac{dE}{dq}$  may be found by implicitly differentiating the first order condition for  $E$  maximizing the Hamiltonian:

$$\frac{dE}{dq} = -\frac{U''_{Eq}(q, E) + \lambda f''_{Eq}(q, E)}{U''_{EE}(q, E) + \lambda f''_{EE}(q, E)} = -\frac{\Theta'(q)}{U''_{EE}(q, E) + \lambda f''_{EE}(q, E)}$$

It follows from the concavity of the Hamiltonian with respect to  $E$  that the sign of  $\frac{dE}{dq}$  is the same as the sign of  $\Theta'(q)$ . In the model used in the main text one can easily verify that  $\left(\frac{\partial f}{\partial q}\right)_{q=q^*} = 0$  and  $\left(\frac{\partial f}{\partial E}\right)_{q=q^*} > 0$ . It follows that the sign of  $\left(\frac{\partial q'}{\partial q}\right)_{q=q^*}$  is the same as the sign of  $\Theta'(q)$  which confirms the stability analysis in the main text.