Managing Genetic Resources for Fun and Profit

– The Role of the Interest Rate in Natural Selection

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We present a bioeconomic analysis of the optimal long-term management of a genetic resource in the presence of selective harvesting. It is assumed that the individuals that possess a particular gene have lower natural mortality rate and are more valuable to catch. Highly selective harvesting may cause such a gene to loose its fitness advantage changing the evolutionary path of the species. Results indicate that the relationship between the natural rate of selection against less valuable individuals and the interest rate are crucial in determining whether the valuable gene should be preserved or allowed to become extinct.
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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 (James E. Wilen, 2000).[1] Resource economists have followed developments in the biological and ecological sciences relatively closely ever since, and have attempted to include them in their own bioeconomic models.

For decades biologists have been aware of the possibility that selective harvesting or hunting could alter the genetic pattern of a resource (Mikko Heino 1998). Resource economists have, however, ignored this issue, presumably on the assumption that the effects were negligibly small. Recent empirical evidence, however, suggests that this is not the case (Trond Haugen and Leif A. Vøllestad, 2001, Mikko Heino and Olav R. Godø 2002, David.

W. Coltman et al. 2003, David O. Conover and Stephan B. Munch 2003). Substantial value may potentially be lost in terms of resource rents if this is not taken into account in the management of renewable natural resources.

In general, all non-random harvesting will result in some degree of genetic selection. Two important cases of selective harvesting have received recent attention in the literature: trophy hunting and fishing. Trophy hunters have preferences for specific physiological traits in their prey, such as body size or the size of antlers or horns (Richard B. Harris et al. 2002). On the other hand the market value of fish depends on their size, which creates incentives for fishers to limit their catch to larger fish. This may effect the distribution of genes within the entire ecosystem.

There is a large literature, both theoretical and empirical, in ecology confirming the effects of human harvesting on the distribution of genes in ecosystems. David Reznick et al. (1990), Thomas H. Thelen (1991), John T. Jorgenson et al. (1993) and 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; and Richard Law (2000), Haugen and Vøllestad (2001), Heino and Godø (2002), and Conover and Munch (2003), among several others, examine fisheries. The evidence suggests that these effects are too large to be neglected. Ecologists have therefore recently started to examine the implications of selective harvesting for optimal resource management (Heino 1998). Ecologists conventionally use Maximum Sustainable Yield (MSY) as the goal of optimal resource management. MSY, however, neglects the time preference of money and may yield misleading policy recommendations (Paul A. Samuelson 1976). It is therefore important to develop optimal resource management of genetic resources within economic theory.

Management of genetic resources is an integral part of biodiversity. A rationale for the interest by economists in 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 in which various measures of biodiversity assign benefits to genetic variation (Martin L. Weitzman 1992, Weitzman 1993), and which considers how to value these benefits and how to regulate ecosystems with diversity measures as policy objectives (Stephen Polasky et al. 1993, Polasky and Andrew. R. Solow 1995). The value assigned 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. A recent exception is William A. Brock and Anastasios Xepapadeas (2003), where plants, varying in their resistance to insect pests, are modeled.

In this paper we examine the optimization problem of a resource manager faced with a resource for which the value of the harvest is completely determined by genes. The genetic model in Brock and Xepapadeas (2003) assumed Hardy–Weinberg equilibrium. The Hardy–Weinberg equilibrium, sometimes referred to as a law, is characterized 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. Based on the knowledge that human harvesting affects the distribution of genes, we will utilize a genetic model where the Hardy–Weinberg equilibrium does not apply, except in steady state. The difference is that in our model resource harvesting affects the *rate* at which natural selection occurs. The difference between the

genetic components of our study and that of Brock and Xepapadeas (2003) is that they employ 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, say, large mammals and fish.

We will use the genetic model to develop a bioeconomic model by which 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, given selective harvesting.

I. A Model with Population and Genetic Dynamics

A. 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 to be driven by the following differential equations:

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

Here r_i is growth rate, δ_i is 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:

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

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.

B. Genetic dynamics

The determination of phenotypes is determined by the gene frequency.[2] 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 is possible. Here it is assumed that individuals of genotype *AA* and *Aa* are of phenotype *G*, and that 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 $(1 - q)^2 + 2q(1 - q) = 1 - q^2$. 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:

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

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:[3]

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

Here *s* is given by (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.

II. 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:

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

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

$$h_G = \gamma x_G E = \gamma\left(1-q^2\right)xE \tag{6}$$

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

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

Instantaneous harvesting is then given by

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

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

$$s = \delta_B-\delta_G-\gamma E \tag{9}$$

To examine the optimal regulation of the natural resource, we assume 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:

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

where ρ is the discount rate. The maximization in Equation (10) is performed subject to:

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

The Hamiltonian for this problem is given by:

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

In addition to the relevant transversality conditions, necessary conditions for an optimal program are given by Equation (11) and:[4]

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

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

The complexity of the condition in (13) and (14) gives 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 $\dot{q} = 0$. $q = 0$, $q = 1$, 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. Further, it turns out in our analysis that a discussion of the steady states $q = 0$ and $q = 1$ is contained in a discussion of $s = 0$, so these cases are not discussed separately. Note that in the steady state, evolution does not select for any of the genes.

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

$$\lambda = -\frac{2pK}{r\rho}(r-\delta_B)(\delta_B-\delta_G)q \tag{15}$$

The steady state value λ is never positive, which is an obvious implication of *B* being unwanted. Inserting this value of λ and $s = 0$ into (13) gives a fourth order polynomial equation for determining steady state value of *q*.

$$\frac{\partial H}{\partial E} = \Theta(q) = \frac{\gamma Kp}{r}\left[a_0 + a_1 q + a_2 q^2 + a_3 q^3 + a_4 q^4\right] = 0 \tag{16}$$

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 in 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*, δ_G, δ_B and ρ. It is straightforward to calculate that $\Theta(1) = 0$, reflecting that the marginal benefit of increasing *E* is zero if there are no animals of phenotype *G* in the population. Thus $q = 1$ is a steady state. The root $q = 1$ can be determined from the expression (11), 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).

$$\begin{aligned}\Theta(0) &= \frac{\gamma Kp}{r}a_0 = \frac{\gamma Kp}{r}\left(r-\delta_B-(\delta_B-\delta_G)\right)\\ \Theta'(1) &= \frac{2\gamma Kp}{r\rho}(r-\delta_B)(\delta_B-\delta_G-\rho)\end{aligned} \tag{17}$$

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 zero 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 ρ, 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. 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. The steady state $q = 0$ is missing from this analysis. If $q = 0$, then there are no copies of the a gene in the population and the model reverts to a standard resource economic model. In the absence of mutations, there is no reason for introducing genetics into the analysis. However, it is interesting to examine the stability properties of the steady state $q = 0$ to examine the behavior of the optimal path for low values of q. Using the same argument as above, it follows that if $\Theta(0) > 0$, then the marginal benefit of increasing E relative to the steady state value is positive. Therefore it is optimal to increase E, and s therefore becomes positive. This implies that $\dot{q}$ becomes positive. $\Theta(0) > 0$ is therefore a condition for the instability of $q = 0$. By the same

reasoning, $\Theta(0) < 0$ is a condition for the stability of the steady state $q = 0$. 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 arguments above indicate 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 . Here, $\Theta(q) > 0$ for all q. The optimal choice of E is therefore always higher than the steady state level of E and $q \to 1$ as $t \to \infty$. For this combination of parameter values, it is always optimal to let the gene A become extinct.

Case 3: $\Theta(0) < 0$ 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 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 3. It shows a steady state in the interior of [0, 1), but this steady state is not stable. Rather, it is a Skiba point (A. K. Skiba (1978).[5]

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

Case 4: $\Theta(0) < 0$ and $\Theta'(1) > 0$. 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 for low levels of *q*. 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. In this case, $\Theta(q)$ may have either zero or two roots in [0,1). It is possible to derive exact conditions for when there are two and when there are no roots in [0, 1). Unfortunately the mathematical formulation of these expressions is rather complex and it is hard to give interesting interpretations. We therefore do not present them here. Let us look at the graphical illustration of each case. Figure 4a 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^*/γ for all values of *q* in order to avoid selecting against the *A* gene.

Figure 4b shows the solution with two roots in [0,1). This happens, for example, for the parameter values: $r = 0.61$, $\delta_G = 0.28$, $\delta_B = 0.45$ 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, or a Skiba point as in Case 3. q_2^* is a stable equilibrium since it is optimal to reduce effort for any $q > q_2^*$ and, conditional on $q(0) > q_1^*$, optimal management will converge to this steady state where both genotypes are present in equilibrium.

III. Concluding Remarks

In this paper we have addressed the optimal management of the genetic resources of a renewable resource. The results 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 regimes of management 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 a reduced frequency of the valuable gene, or even extinction, is the optimal solution.

Our results show that current management regimes for renewable natural resources that are subject to selective harvesting may lead to suboptimal solutions. This is most likely to happen for resources where the non-targeted phenotypes have low intrinsic growth rates, which is the case for many economically important properties such as the size of individual animals. Further, mismanagement becomes more likely if selective harvesting has substantially reduced the frequency of the preferred gene, either through a long period of selective harvesting or high selection pressures. Managers of such resources should clearly reevaluate their management strategies, since current management may lead to extinction of valuable genes as the optimal policy.

There are two simplifications in the present model the inclusion of which affects the result. First, the productivity and cost of harvesting are not affected by the composition of the stock. It seems reasonable to suspect that this is not the case, when, for example, 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 there is no harvesting of phenotype *B*. This simplification describes trophy hunting fairly well, but is a poor description of many renewable natural resources such as fisheries. The management of genetic resources is very relevant in fisheries, as technological improvements allow more selective fishing, and this assumption should be challenged in future works. 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.

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:

(A1) $$\max \int_0^{\infty} U(q,E)e^{-\rho t}dt \;\; s.t. \dot{q} = f(q,E),\; q(0) \text{ given.}$$

Along the optimal path, $\dot{q} = f\left(q, E(q)\right)$. 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

(A2) $$\left(\frac{d\dot{q}}{dq}\right)_{q=q^*} = \left(\frac{\partial f}{\partial q}\right)_{q=q^*} + \left(\frac{\partial f}{\partial E}\right)_{q=q^*}\left(\frac{dE}{dq}\right)_{q=q^*} < 0$$

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

(A3) $$\frac{dE}{dq} = -\frac{U''_{Eq}(q,E) + \lambda f''_{Eq}(q,E)}{U''_{EE}(q,E) + \lambda f''_{EE}(q,E)} = -\frac{\Theta'(q)}{U''_{EE}(q,E) + \lambda f''_{EE}(q,E)}$$

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 $\left(\frac{dq'}{dq}\right)_{q=q^*}$ is the same as the sign of $\Theta'(q)$, which confirms the stability analysis in the main text.

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Figure Captions

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

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

Figure 3. $\Theta(q)$ for Case 3.

Figure 4a. $\Theta(q)$ for Case 4 with no roots in [0, 1).

Figure 4b. $\Theta(q)$ for Case 3 with two roots in [0, 1).

Figures

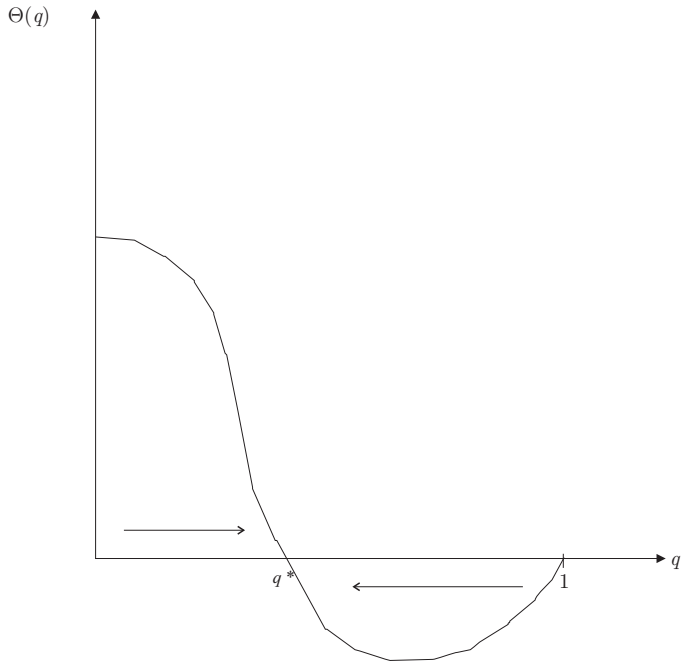


Figure 1

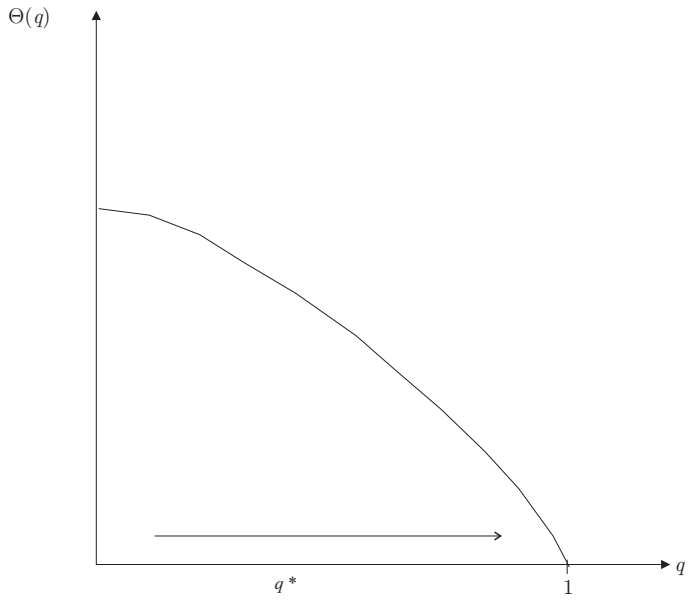


Figure 2

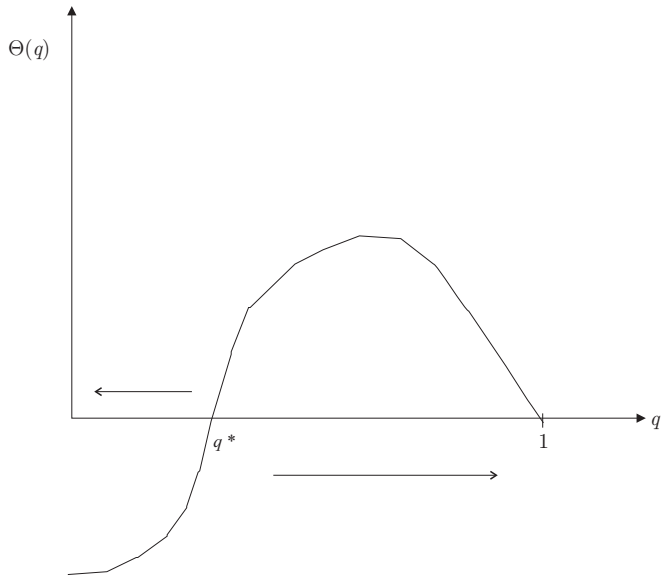


Figure 3

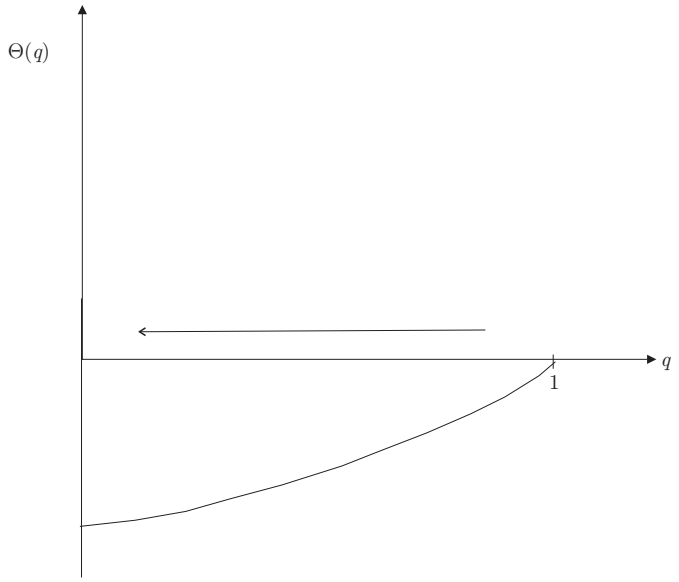


Figure 4a

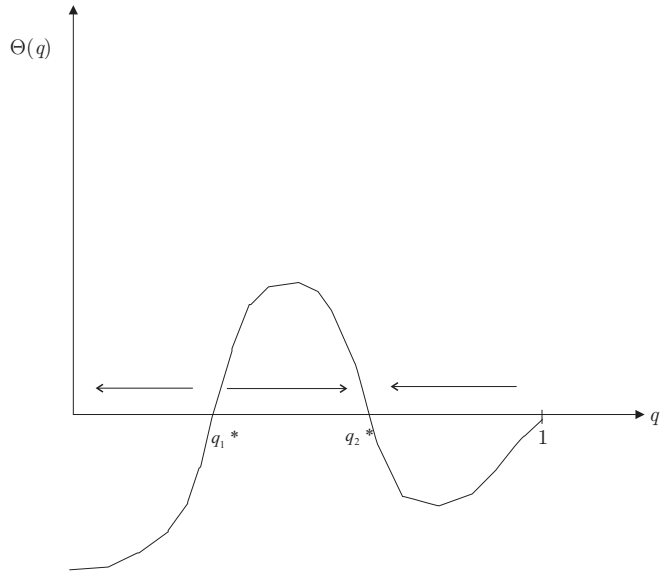


Figure 4b

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[1] Wilen (2000) especially mentions the articles by Rodney J. H. Beverton and Sidney J. Holt (1957) and Milner B. Schaefer (1957) in biology, and by H. Scott Gordon (1954) and Anthony D. Scott (1955) in economics.

[2] There is an important issue that is suppressed here. Here all of the phenotypic variation is ascribed 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 one such environmental factor.

[3] This is a basic result in quantitative genetics. See, e.g., Douglas Falconer and Trudy F. Mackey (1996) for an exposition.

[4] 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.

[5] There has recently been an increasing interest in Skiba points in the resource economic literature on non-linear natural resource problems. See, e.g., William A. Brock and D. Starrett (2003) or Anne Sophie Crépin (2003). The results presented in these papers are consistent with the conclusions presented here.