Optimal management of renewable resources with Darwinian selection induced by harvesting

Atle G. Guttormsen a, Dadi Kristofersson a,b, Eric Nævdal c,*

a Department of Economics and Resource Management, Norwegian University of Life Sciences, P.O. Box 5003, N-1432 Aas, Norway
b Institute of Economic Studies, University of Iceland, Arogata 14, 101 Reykjavik, Iceland
c Department of Economics, University of Oslo, P.O. Box 1095 Blindern, 0317 Oslo, Norway

ABSTRACT

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 individuals possessing a particular gene have a lower natural mortality rate and are more valuable to capture. Highly selective harvesting may cause such a gene to lose its fitness advantage, and hence change the evolutionary path of the species. Results indicate that in a zero-cost harvesting regime, the decision to preserve the valuable gene depends on the natural rate of selection against less valuable individuals and the interest rate. On the other hand, the decision to let the less valuable gene become a significant fraction of the genes depends only on biological parameters. If marginal costs are positive, it is never optimal to let a valuable gene become extinct. Further, for some parameter values, the system exhibits multiple equilibria. Therefore, optimal regulation may depend on initial conditions.

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For decades, biologists have been aware of the possibility that selective harvesting could alter the genetic pattern of a resource [12]. Recent empirical evidence suggests that this effect is substantial [4,5,11,14,21] and that this issue deserves more attention from resource economists. Potentially, substantial value may be lost in terms of resource rents if genetic resources are not considered in the management of renewable natural resources.

In principle, all nonrandom 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 selective fishing. First, trophy hunters have preferences for specific physiological traits in their prey, such as body size or the size of antlers or horns [10]. Other examples of the effects of hunting on gene frequencies are provided by [12,15,17,26,30,31]. Second, there is the selective nature of commercial fishing, which often targets traits such as catchability or size, as discussed in Refs. [5,11,13,14]. Some of these papers have examined the implications of selective harvesting for optimal resource management and maximum sustainable yield (MSY) [13]. However, as MSY can be a desirable goal only if the opportunity cost of capital is zero, it may result in misleading policy recommendations [27].

The management of genetic resources has received some attention in the resource economics literature. First, some authors have discussed the management of genetic resources as an integral part of biodiversity. Refs. [33,34] assigned benefits to genetic variation, whereas Refs. [24,25] considered how to value these benefits and how to regulate ecosystems with diversity measures as policy objectives. Second, Refs. [18,19] modeled the evolution of resistance to pathogens.

* Corresponding author. Fax: +47 22958825.
E-mail addresses: atle.guttormsen@umb.no (A.G. Guttormsen), dmk@hi.is (D. Kristofersson), eric.navdal@econ.uio.no (E. Nævdal).

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However, the genetic models used in these papers are somewhat more suitable to organisms that reproduce nonsexually as the models are not directly rooted in the Mendelian genetics of sexually reproducing species. Third, Ref. [2] modeled the economic value of genetic diversity through the value of the services provided by the genes. This is a model where a pest may develop resistance to agricultural commodities that are genetically modified to be pathogenic to the pest. The model used in Ref. [2] explicitly assumed sexual reproduction.

To a large extent, managing genetic resources in nature is equivalent to managing genetic selection and evolution. Therefore, a suitable model must have a population genetics component. In this paper, we examine the optimization problem of a resource manager faced with a biological resource, the value of which depends on the genetic composition of the individuals in the resource. We introduce a genetic model into a classic bioeconomic model to 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 depends solely on the profits generated by harvesting, given selective harvesting. Models of harvesting-induced selection for animals must recognize that harvesting of sexually reproducing species occurs and that it requires the use of genetic models of sexual reproduction, which unfortunately implies complicated nonlinear models. The model presented here is, to our knowledge, the first economic model to examine the effect of selective harvesting on the genetic configuration of the harvested species and the second, after Ref. [2], to explicitly consider the genetics of a sexually reproductive species. Our model shares some features with Ref. [2] in that we both present a model where a sexually reproducing species is subject to genetic selection mechanisms. Our model differs from Ref. [2] in that we combine the genetic model of the species with a population model of the species that is subject to selection.1 In addition, our work differs from the previous literature in that we emphasize the possibility and implications of multiple equilibria in the management of genetic resources.

Our model may be thought of as describing the optimal management of a pelagic fishery, involving fish such as capelin or anchovy, mainly used in the production of fishmeal. Fishmeal is an important ingredient in feed for poultry, pigs and carnivorous farmed fish such as salmon, and has proven to have few substitutes. However, regardless of the increasing demand for fishmeal, the world catch has not increased over the past 20 years, and has in fact been declining in the past few years [16]. This indicates that world pelagic fish stocks are under considerable harvesting pressure. In general, there has been widespread concern among scientists regarding harvesting pressure and the consequences that it has for biodiversity and ocean ecosystems [22,36].

An individual capelin or anchovy is small and its market value is low. However, pelagic fisheries are profitable owing to the tendency of pelagic fish to form large groups, known as schools, which permits the simultaneous capture of large numbers of individuals. In fact, it is unlikely that commercial harvesting would be possible if schooling did not occur. These schools represent adaptations to the natural environment where the individuals in schools obtain advantages such as less energy use and reduced mortality [23]. Although the schooling behavior reduces mortality in the absence of fishing, fishing may negate this advantage and cause a reduction in the frequency of genes that control schooling behavior. For simplicity, we assume that the behavioral impetus to form schools is controlled by variations in a single gene. Our model addresses the question of how to manage such a resource, given that there exists a mutated gene, which suppresses the behavioral impulse to form schools. This interpretation allows an analytically tractable model that is also relevant to important real-world resource management problems.

The topic necessitates some use of nomenclature that may be unfamiliar to some economists, so a brief glossary is provided in Appendix A.

1. A model with population and genetic dynamics

1.1. Population dynamics

Consider a population with two phenotypes, labeled “bad” (B) and “good” (G). The B phenotype is labeled “bad” as it is assumed that fish of this type have no harvest value. The G phenotype is labeled “good” because fish of this type have economic value to fishermen.2 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:

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

(1)

Here, $r_i$ and $\delta_i$ are the growth rate and the mortality rate, respectively, with both being 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 $\dot{x} = x_G + x_B$. We want to consider the regulation of the population when different phenotypes have a different biological productivity. It is assumed that phenotype B is biologically less productive than phenotype G. We model this by assuming that $r_B = r_G = r$ and $h_B = h_G$.

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1 In Ref. [2], there is a population dynamics model of plants, but there is not one of the pest.
2 There are two sets of assumptions that could lead to this particular phenotype. One can assume that the price of the bad phenotype is zero and that no individuals of this phenotype are caught as bycatch. Alternatively, one can assume that the catchability coefficient of the bad phenotype is zero. It is the latter interpretation that is intended here.
that $\delta_c < \delta_B < \tau$. The expression $r - \delta_B$ is the intrinsic growth rate of phenotype $B$ and will be important in the following analysis.\(^3\) Further, it is assumed that the number of individuals is equally proportional to the biomass for both phenotypes and that 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 becomes of importance below is the selection coefficient, $s$. Formally, $s$ is defined as the percentage contribution of one phenotype to the next generation. More explicitly, this implies that if phenotype $G$ contributes 100 individuals to the next generation, then phenotype $B$ contributes $100 \times (1-s)$ individuals. From Eq. (1), it follows that $s$ is given by

$$s = \frac{x_G - x_B}{x_B} = - (\delta_c - \delta_B) - \frac{h_G}{x_G} + \frac{h_B}{x_B}. \tag{2}$$

In the absence of harvesting, $s = s^* = \delta_B - \delta_c > 0$, indicating that $G$ is selected for, where $s^*$ 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 $x_C = k(1-\delta_c/r)$. However, if the harvesting effort directed at phenotype $G$ is sufficiently large relative to the harvesting effort directed at phenotype $B$, then $s$ changes sign and $G$ is selected against, leading to a reduction in the $x_C$ stock and even the extinction of phenotype $G$. Therefore, there is a risk that genetic resources will be mismanaged if they are not properly considered in management strategies. It is this possibility that is the main motivation for this paper.

### 1.2. Genetic dynamics

The phenotypes are determined by the gene frequency.\(^4\) The genetic model described below is explained in detail in Ref. [9], Chapter 2. The model is a standard model of Mendelian genetics. 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 number of variations are possible.\(^5\) We assume that individuals of genotype $AA$ and $Aa$ are of phenotype $G$ and that individuals of genotype $aa$ are of phenotype $B$. In the language of geneticists, the $A$ allele exhibits complete dominance with respect to fitness. This allele gives rise to the good phenotype and we refer to it colloquially as the “good gene” or the “$G$ gene”. Let the frequency of $a$ be $q$. As it is the $a$ allele that gives rise to the bad phenotype, we refer to this allele as the “bad gene” or the “$B$ gene”. Under the assumption that mating between genotypes is nonpreferential 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 $q^2$. Hence, the fraction of $x$ that is $x_C$ is $(1-q)^2 + 2q(1-q) = 1-q^2$. It follows that $x_C = (1-q^2)x$ and $x_B = q^2x$. Further, we assume that only the individuals of type $G$ can be harvested commercially owing to their tendency to group into large schools. On the other hand, individuals of type $B$ do not form schools but are dispersed in the ocean and cannot be targeted by fishermen. This leads to perfectly selective harvesting of type $G$ individuals. Thus, $h_B = 0$. Therefore, the changes in $x$ are determined by the following differential equation:

$$\dot{x} = nx(1 - \frac{x}{x_C}) - \delta_C(1 - q^2)x - \delta_B q^2x - h_G. \tag{3}$$

Because of the evolutionary pressure imposed by selection, $q$ may be a nonconstant function of time. The following differential equation can be derived from standard results in quantitative genetics (see Appendix B):

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

where $s$ is given by Eq. (2). From Eq. (4), it is obvious that if the constant $s$ is not zero, then there are only two steady states, $q = 0$ and $1$. If $B$ is selected against, then $s$ is positive and $q$ approaches 0 for any initial value of $q$ in the absence of harvesting. If $s$ is negative, then $G$ is selected against and $q$ converges to 1.

Since the bad gene would become extinct in the absence of harvesting in this model, the reader may wonder why it is there in the first place. Mutations occur continuously and as the $B$ gene is assumed recessive, it is not selected against as long as it is paired with a copy of the other gene in heterozygotes. This gives the $B$ gene a place to hide, so to speak. Therefore, it can persist for a long time in a population even if it is selected against. This is a general result in genetics and it

\(^3\) Our model avoids a possible ambiguity with respect to the terms “bad” and “good.” In our model, “bad” and “good” are terms of economic value. Some biologists would use “good” to describe the phenotype with the highest biological productivity. In our model, the economically “good” phenotype is also the biologically most productive. In some real-life situations, phenotypes that are rare because of low biological productivity could very well be particularly valuable to hunters because of their rarity.

\(^4\) Here, all of the phenotypic variation is ascribed to genetic variation. In the real world, part of the morphological variation is due to phenotypic plasticity. Phenotypic plasticity is the morphological variation that is possible within a single genetic variety. This plasticity is caused by environmental factors. The frequency of different phenotypes in itself may be one such environmental factor. It is also well known in ecology that if a population is small, the effect of evolutionary selection becomes weak relative to random genetic drift. Thus, our model is only appropriate for situations where the sum of individuals belonging to the two phenotypes is reasonably large. Animals, in particular mammals, may also respond to human harvesting through cognitive processes. The economic implications of this are discussed in Ref. [20].

\(^5\) In fact, there are seven possibilities. If each individual genotype represents a unique phenotype, there are three phenotypes. If all genotypes belong to the same phenotype, there is obviously one. There are three possible ways where two genotypes belong to a specific phenotype and one genotype is a unique phenotype.
explains, for example, the existence of certain rare genetic disorders. However, if fishing implies that the \( G \) gene is selected against, the fishermen attach equal value to the animals with \( AA \) and \( Aa \) combinations, so \( A \) is not safe in any genotypic form. This makes the \( A \) gene much more vulnerable to being selected against than the \( a \) gene, which explains why the \( A \) gene can be rapidly driven out of a population, whereas the \( a \) gene can persist for a long time.

The model has some similarities to multispecies models with competing species ([Ref. [3], Chapter 10.2]) and models of fish stocks of a single species that are divided into substocks, with limited or no reproductive interaction, [29]. The model presented in Ref. [29] captures a variety of hereditary behavior, where behavior patterns are transmitted from generation to generation through possibly imperfect learning. However, there is no genetic component in the model presented in Ref. [29] so it is inadequate to model behavior transmitted through genes.

In a certain sense, the different phenotypes compete for the same resource that is available in amount \( K \). However, note that competition for resources between individuals of the two phenotypes is the same as competition for resources between individuals of the same phenotype. This assumption would be too strong in some real-world cases, where different phenotypes are drawn to different resources. The fundamental difference between our model and multispecies and substock models is that, in our model, individuals belonging to one phenotype reproduce randomly, with individuals of both phenotypes. This is vitally important because the bad phenotype contributes to the growth of the superior phenotype through heterozygotes, interlinking the two in a manner quite different from the multispecies and substock models. We comment further on the similarities between competing species models and our model in the summary.

In the following analysis, three expressions will be of crucial importance. First, the expression \((r-\delta_h)\) gives the intrinsic productivity of phenotype \( B \). It measures how fast phenotype \( B \) regenerates in the absence of density dependency effects. This is an absolute measure of the biological productivity of phenotype \( B \). Second, the expression \((\delta_h-\delta_c)\) denotes the selection in the 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 \( G \), as only phenotype \( G \) is of value and the stock size is in a steady state. The third part is simply the discount rate, \( p \), which measures the opportunity cost of capital. The relative magnitude of these expressions together will determine whether phenotype \( B \) will establish itself permanently in the population and whether it will drive phenotype \( G \) to extinction.

2. Optimal management

For most species, genetic dynamics are relatively slow compared to population dynamics. We assume that the population at every point in time is at a population dynamic equilibrium determined by \( x = 0 \). By making this assumption, we do not mean that \( x \) does not change with time. Rather, it is assumed that \( x \) responds to changes in \( h \) and \( q \) so immediately and so quickly that \( x \) is always in biological equilibrium. It responds infinitely rapidly to changes in \( h \) and \( q \) on the timescale of the genetic changes. Whenever \( q \) or \( h \) changes, \( x \) will instantaneously move to a new steady-state level defined by \( x = 0 \). Then it follows from Eq. (3) that

\[
h_c = rx \left( 1 - \frac{x}{K} \right) - \delta_c (1 - q^2)x - \delta_h q^2 x.
\] (5)

It is assumed that the harvesting depends on harvesting effort \( E \) such that

\[
h_c = \gamma x E = \gamma (1 - q^2) x E,
\] (6)

where \( \gamma \) is the catchability coefficient. Combining Eqs. (5) and (6) yields

\[
x = \frac{K}{r} (r - \delta_c - \gamma E) + \frac{q^2 K}{r} (\delta_c - \delta_h + \gamma E).
\] (7)

Then, instantaneous harvesting is given by

\[
h_c = \frac{\gamma (1 - q^2) K}{r} (r - \delta_c - \gamma E) + \frac{q^2 (\delta_c - \delta_h + \gamma E) E}{r}.
\] (8)

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

\[
s = \delta_h - \delta_c - \gamma E.
\] (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. The cost of effort is assumed to be \( C(E) = cE \) and the catch is assumed to be valued at an exogenous price \( p \). Then, the objective function is

\[
\max_{E} \left( \int_{0}^{\infty} (p h_c - cE) e^{-pt} dt \right) = \max_{E} \left( \int_{0}^{\infty} p \left( \frac{\gamma (1 - q^2) K}{r} (r - \delta_c - \gamma E) - q^2 (\delta_h - \delta_c - \gamma E) E - cE \right) e^{-pt} dt \right).
\] (10)
where $\rho$ is the discount rate. The maximization in Eq. (10) is performed subject to

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

The Hamiltonian for this problem is given by

$$H = \frac{pq}{r}((r - \delta - \gamma E) - q^2(\hat{q} - \delta - \gamma E))E + \lambda \left(\frac{q^2(1-q)(\hat{q} - \gamma E)}{1 - (\hat{q} - \gamma E)q^2}\right). \quad (12)$$

In addition to the relevant transversality conditions, the necessary conditions for an optimal program are given by Eq. (11) and

$$\frac{\partial H}{\partial \hat{q}} = \frac{pq}{r}((r - \delta - \gamma E) - q^2(\hat{q} - \delta - \gamma E)) - cE + \lambda \left(\frac{q^2(1-q)q^2}{1 - (\hat{q} - \gamma E)q^2}\right) = 0, \quad (13)$$

$$\lambda = \frac{2pqKE}{r}((r - \delta - \gamma E) + (1-q^2)(\hat{q} - \delta - \gamma E)) - \frac{2pqKE}{r} \hat{s} + \frac{\lambda(\hat{q} - \delta - \gamma E)}{1 - (\hat{q} - \gamma E)q^2} = 0. \quad (14)$$

The system in Eqs. (13) and (14) is too complex to solve explicitly. Further, isolating $E$ in Eq. (13) involves solving a cubic polynomial. It will be shown below that optimal paths are qualitatively sensitive to changes in parameters and may have multiple steady states. In order to enumerate and describe the steady states, it turns out to be effective to start with the case where harvesting is costless. In this case, the conditions in Eq. (11) have a structure that enables us to find and characterize steady states with relative ease. With this special case as a starting point, results that are more general are derived for costly harvesting.

### 3. Zero-cost harvesting

From Eq. (11), it is evident that there are three conditions under which $\dot{q} = 0$: $q = 0$, $q = 1$ and $s = \hat{q} - \delta - \gamma E = 0$. In the first two cases, either of the genes can be absent from the population. The case where $s = 0$ is the most interesting, as both genes are present in the population. Obviously $s = 0$ implies that

$$E = E^* = \frac{\hat{q} - \delta}{\gamma}. \quad (15)$$

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, gene frequency is constant over time. Biologically, this implies that both genes are equally successful and there is no selection.

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

$$\lambda^* = -\frac{2pq}{\rho} (r - \delta)(\hat{q} - \delta)q. \quad (16)$$

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

$$\frac{\partial H}{\partial \hat{q}} = \rho \Theta(q) = \frac{\gamma p q K}{r} [a_0 + a_1 q + a_2 q^2 + a_3 q^3 + a_4 q^4] = 0. \quad (17)$$

Here, $a_0 = (r - \delta)(\hat{q} - \delta \gamma c)$, $a_1 = 0$, $a_2 = -(r - \delta q) + 2(\hat{q} - \delta \gamma c)$, $a_3 = -(2/\rho)(r - \delta q)(\hat{q} - \delta \gamma c)$ and $a_4 = 1/\rho (2(r - \delta q) - \rho)(\hat{q} - \delta \gamma c)$. The expression $\Theta(q)$ is the derivative of the Hamiltonian with respect to $q$ after inserting the steady-state values of effort $E^*$ and the shadow price $\hat{r}^*$.

### Proposition 1

Let $q^*$ be a steady-state value of $q$ to the problem in Eq. (10). Then, $q^*$ is locally stable if $\Theta(q^*) < 0$. Conversely, $q^*$ is unstable if $\Theta(q^*) > 0$. The four possible combinations of numbers of steady states and stability properties are summarized in Table 1, and illustrated in Fig. 1. Case 1 corresponds to $r - \delta > \delta - \delta c$ and $\delta - \delta c > \rho$. The first inequality indicates that phenotype $B$ has higher intrinsic productivity than the internal rate of return on preserving phenotype $C$. Some $q > 0$ is therefore optimal. The second inequality indicates that the internal rate of return is higher than the alternative value of capital. Therefore, extinction of the good gene cannot be optimal. The only stable steady state, according to Proposition 1, is the interior solution $q^*$. Case 2 corresponds to $r - \delta > \delta - \delta c$ and $\delta - \delta c < \rho$. The first inequality is the same as for Case 1. 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 only stable steady-state solution is \( q = 1 \). Case 3 corresponds to \( r - \delta_B < \delta_B - \delta_C \) and \( \delta_B - \delta_C < \rho \). 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. The stable steady states are \( q = 0 \) and \( q = 1 \) while the interior solution is unstable. Case 4 corresponds to \( r - \delta_B < \delta_B - \delta_C \) and \( \delta_B - \delta_C > \rho \). As for Case 3, the first inequality implies that a positive value of \( q \) is not optimal for low levels of \( q \). The second inequality implies that the internal rate of return is greater than the alternative value of capital so extinction of type \( G \) cannot be optimal. There may therefore be either no or two roots in \((0,1)\). When there are two roots, labeled \( A \) in the figure, the stable steady states are \( q = 0 \) and \( q_1^{*} \) while \( q_2^{*} \) and \( q = 1 \) are unstable, in accordance with Proposition 1 case where there are no roots in \((0,1)\), labeled \( A \), \( q = 0 \) is stable and \( q = 1 \) is unstable.

Intuitively, we can deduce the stability properties of a given steady state from the sign of \( \Theta'(q) \) by noting that \( \Theta(q) \) is the instantaneous marginal benefit of effort \( E \) evaluated at the steady-state value of effort \( E = (\delta_B - \delta_C)^{-1} \). This implies that close to the steady-state values of \( q \), \( \Theta(q) \) is close to the marginal benefit of an increment in effort relative to the steady-state effort level \( E \). Thus, if \( \Theta'(q) < 0 \), then 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 \( q \), this implies that \( q \) will increase and move towards \( q^{*} \). For values of \( q \) that are slightly larger than \( q^{*} \), \( \Theta(q) < 0 \), so it pays to decrease \( E \) slightly relative to the steady-state value of \( E \). Then, \( q \) will be negative and move towards \( q^{*} \). It follows that \( q^{*} \) is a stable steady state. Conversely, if \( \Theta'(q) \) is positive
(respectively, negative), then to the left (right) of \( q^* \), it pays to decrease (increase) \( E \) relative to \( E^* \). It follows that \( q^* \) is unstable in this case. By the same reasoning, \( q = 1 \) is unstable if \( \Theta'(q) < 1 \) and stable if \( \Theta'(q) > 1 \).

The steady state \( q = 0 \) is missing from this analysis. If \( q = 0 \), then there are no copies of the allele 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 \( q \). If \( \Theta(0) > 0 \), then the marginal benefit of decreasing \( E \) in the steady-state value is positive. Therefore, it is optimal to increase \( E \), and \( s \) therefore becomes positive. This implies that \( q \) becomes positive. Therefore, \( \Theta(0) > 0 \) is 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 \( q = 0 \). 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 \( q = 0 \). Therefore, if \( \Theta(0) > 0 \), one would want to increase \( E \) relative to the \( E^* \) values of \( q \) that are close to zero and therefore \( q \) will increase until it converges towards some stable steady state where \( q = q^* \). Conversely, if \( \Theta(0) < 0 \), one would want to decrease \( E \) relative to \( E^* \) for values of \( q \) that are close to zero and therefore \( q \) will decrease and converge towards \( q = 0 \).

The discussion of the stability properties of \( q = 0 \) and \( 1 \) are formalized in the following propositions:

**Proposition 2.** If \( \delta_B - \delta_G > \rho \), the bad phenotype will not take over the population under an optimal management regime.

**Proof.** Since \( \Theta'(1) = (2r/K) - \delta_B - \delta_G - \rho \) and \( r - \delta_B > 0 \) by assumption. This implies that \( r - \delta_B > \delta_B - \delta_G - \rho \) and that \( \Theta'(1) > 1 \) if \( \Theta'(0) > 0 \) and \( \Theta'(0) < 0 \) implies that \( \Theta'(1) < 1 \) if \( \Theta'(0) < 0 \). Therefore, \( q = 1 \) is an unstable steady state and \( q \) will never converge to \( q = 1 \); so long as the initial value of \( q < 1 \), the population will always contain individuals of the good phenotype.

**Proposition 3.** If \( r - \delta_B > \delta_B - \delta_G \), the bad phenotype will be able to establish a significant population under an optimal management regime.

**Proof.** Since \( \Theta(0) = (r/K) - \delta_B - \delta_G \), \( r - \delta_B > \delta_B - \delta_G \) implies that \( \Theta(0) > 0 \). Then, \( q = 0 \) is an unstable steady state and if the bad gene \( a \) is present in the population, \( q \) will diverge from \( q = 0 \). As long as \( q > 0 \), the population will contain individuals of the bad phenotype.

It follows from Proposition 2 that \( \delta_B - \delta_G < \rho \) is a necessary condition for the bad gene taking over the population under an optimal management scheme. As mentioned, the expression \( \delta_B - \delta_G \) may be interpreted as the internal rate of return on preserving phenotype \( G \), as it is the rate at which it naturally drives out phenotype \( B \). If this return is lower than the interest rate, which specifies the required *external* rate of return, it may be optimal to let phenotype \( G \) become extinct. It follows from Proposition 3 that \( r - \delta_B < \delta_B - \delta_G \) is a necessary condition for the bad gene being unable to establish itself in the population.

There is an interesting contrast between Propositions 2 and 3. The decision to preserve the good gene depends on the economic parameter \( \rho \) and how it relates to the biological parameters. The decision to let the bad gene become a significant fraction of the genes depends only on biological parameters.

### 4. Optimal harvesting with positive effort costs

While introducing costly effort results in considerable algebraic complexity, the model may be analyzed graphically as in Fig. 1. We state without proof that if cost of effort \( c(E) \) is a positive constant \( c \), the polynomial \( \Theta(q) \) may be written as

\[
\Theta(q) = \frac{\gamma K}{r} [a_0 + a_1 q + a_2 q^2 + a_3 q^3 + a_4 q^4] - c. \tag{18}
\]

The effect of effort cost on the original \( \Theta(q) \) in Eq. (17) is to shift it downwards by an amount \( c \) as illustrated in Fig. 2.

There are some distinct differences between solutions from Eqs. (17) and (18). First, \( q = 1 \) is no longer a root of \( \Theta(q) \) and therefore it is never optimal to allow the good gene to become extinct. Further, a positive \( c \) never leads to an increased number of steady states, but may decrease the number of steady states. However, the stability properties of each steady state are preserved, except in the case where \( c \) becomes so large that only \( q = 0 \) remains in a steady state. If this happens, \( q = 0 \) may switch from being unstable to being stable. This may happen in Cases 1 and 2 in Fig. 2.

So far, we have not demonstrated that the paths satisfying the necessary conditions actually exist. These issues will be addressed using numerical analysis and drawing phase diagrams for \( q \) and \( \lambda \) for the cases discussed above. The computations are made with a MATLAB program, which is available through JEE’s online archive of supplementary material, which can be accessed at http://www.aere.org/journal/index.html. The analysis is based on \( \Theta(q) \), with costs as described in Eq. (18) and depicted in Fig. 2. There are four figures labeled as Figs. 3–6 each one corresponding to one of the cases in Fig. 2. The dotted lines indicate the nullclines for \( q = 0 \), whereas the dashed lines indicate the nullclines for \( \lambda = 0 \).

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9 It should be noted that the nature of this shift is robust to more general cost functions. If \( E' \) is the value of \( E \) that solves \( s = 0 \), then similar shifts may be obtained by exchanging \( c \) with \( C(E') \).
The gray shaded area indicates the combinations of $q$ and $l$ such that the value of $E$ that maximizes the Hamiltonian is zero. Finally, the solid black line indicates the stable manifold and its direction. In Figs. 5 and 6, the stable manifold lies closer to the $d\lambda/dt = 0$ nullcline over the intervals between the origin and the steady states labeled SS. Over these intervals, the manifolds have been manually redrawn for legibility.

**Fig. 2.** The effect of positive marginal effort cost. In each of the four cases, $\Theta(q)$ is shifted downwards by a positive marginal cost.

**Fig. 3.** Phase diagram of $q$ and $\lambda$ for $\Theta(q)$ as depicted in Case 1 of Fig. 2.
First, we examine the case in which $Y(0) > 0$ and $Y(1) > 0$, Case 1 in Fig. 2. The phase diagram is presented in Fig. 3. This case comes close to the standard phase diagram in resource economics textbooks. There is a steady state where the nullclines intersect. This steady state clearly has the standard saddle-point property. Evidently, for sufficiently high values of $q$, it pays to postpone all fishing activities until the good gene has recovered to levels that are sustainable with positive harvest.

The case in which $Y(0) > 0$ and $Y(1) < 0$, Case 2 in Fig. 2, is illustrated in Fig. 4. It is similar to Case 1 in that there is a single stable steady state that exhibits saddle-point properties.
The case in which $\Theta(0) < 0$ and $\Theta'(1) < 0$, in which there are two roots in $(0,1)$, Case 3 in Fig. 2, is illustrated in Fig. 5. There are three steady states located at $q = 0$, $q \approx 0.68$ and $q \approx 0.89$. The steady state at $q \approx 0.68$ appears to be an unstable steady state. If $q(0)$ is smaller than this steady-state value, optimal management leads to a path that converges to $q = 0$. If $q(0)$ is larger than this steady-state value, $q$ converges to the high steady state where $q \approx 0.89$. Note that there are no stable manifolds bypassing this steady state and converging to any of the other steady states. Assuming that optimal paths actually exist for all possible values of $q(0)$ and that necessary conditions are therefore satisfied, it must hold that, at the middle steady state, a regulator is indifferent between paths that converge to the low steady state $q = 0$ and the high steady state $q \approx 0.89$. Such points are termed Skiba points [28]. The implications of Skiba points in resource management problems have received attention recently in the resource economic literatures [1,6]. See Ref. [28] for the seminal treatment and Ref. [32] for a technical discussion of Skiba points and their properties. In these articles, the unstable steady states are unstable spirals that do not necessarily coincide with the Skiba points. Here, the unstable steady state is an unstable node in which case the Skiba point coincides with the unstable state. It may be shown that, in optimal control models, unstable steady states are either unstable spirals or unstable nodes [35].

Finally, the case in which $\Theta(0) < 0$ and $\Theta'(1) > 0$, denoted as Case 4A in Fig. 2, is illustrated in Fig. 6. There are two roots in $(0,1)$ and three steady states. Again, the middle steady state is an unstable node and a Skiba point, whereas the two others are stable.

The phase diagrams in Figs. 3–6 have interesting economic interpretations, based on the interpretation of the stable manifold as mapping from $q$ to the shadow price or the marginal value of $q$. Indeed, the shadow price may be interpreted as indicating the optimal tax on a marginal increase in the frequency of $q$ in the fish population if the fishery is competitive. However, the implementation of such a tax requires care, since the level of the tax depends on whether the catch consists of heterozygotes or homozygotes in the good gene.

The manifold intersects the origin in all four cases, which implies that for values of $q$ that are close to zero, the shadow price is also close to zero. The interpretation is straightforward. For low values of $q$, the fraction of the fish stock that is bad is $q^2$. Most of the copies of the bad gene will be mated to copies of the good gene. Also, the rate of increase in the fraction of fish that is bad will be low, because $q$ and $q^2$ will grow slowly for low values of $q$. For high values of $q$, the result is more complex. In Cases 1 and 4, the shadow price becomes rapidly more and more negative as $q$ increases, whereas in Cases 2 and 3, the shadow price increases with $q$, reflecting the fact that the marginal damage becomes smaller as $q$ approaches 1. These differences are perhaps best understood by recalling the results from the costless fishery. There, it was optimal to let the good gene become extinct in Cases 2 and 3, i.e., to let $q$ approaches 1, whereas there were stable steady states with $0 < q < 1$ in Cases 1 and 4. We can therefore delineate the motivations for having $q < 1$ in the different cases. In

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10 One may imagine that a bad gene does not exist in a population until some random point in time when a mutant is introduced. This raises the question of whether harvesting effort should be moderated prior to the existence of such a mutant in order to prevent it from gaining a foothold. This question is beyond the scope of this article. In the present model, the fact that the shadow price of the bad gene is close to zero for low values of $q$ implies that if the existence of the mutant can be detected at low levels of $q$, such a precaution is not desirable. This result, which depends on our genetic model, may not be robust.
Cases 1 and 4, we want to reduce $q$ to restore a profitable fishery. In Cases 2 and 3, we restore the fishery because it is too costly to harvest as $q$ approaches 1. Obviously, in Cases 1 and 4, the marginal damage of $q$ is much higher if the motivation is to restore a fishery rather than if the fishery is just too expensive to deplete completely.

5. Concluding remarks

In this paper, we have addressed the optimal management of genes in 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 results presented here share some features with the competing multispecies model and model of stocks that are divided into substocks. Harvesting in such cases may give the biologically less competitive species of substock an advantage that enables it to sustain a viable population or even make the biologically more competitive species extinct [3,29]. The same may happen with the less competitive phenotype in our model. However, the fact that the phenotypes belong to the same sexually reproducing species makes the dynamics of this process rather different, as it opens up the possibility of Skiba points occurring. To our knowledge, these points have not been shown in multispecies harvesting models except for models where nonlinear biological growth functions imply multiple steady states [6]. The model identifies two important determinants of optimal management, one for a case where there is a small share of a bad gene and another for a case where the bad gene is a large share. Whether the frequency of the bad gene is allowed to increase initially depends only on biological parameters. If the intrinsic growth rate of the bad phenotype exceeds the internal rate of return in the resource, it is optimal to allow a bad gene to establish a significant presence in the population. On the other hand, if the internal rate of return in the resource exceeds the discount rate, the bad gene should not be allowed to take over the entire population in a zero cost fishery. In other words, the optimal preservation of the wanted gene depends on the relationship between the discount rate and the biological parameters. We identified four different solutions to the problem. Two solutions are of special interest to current regimes of natural resource management. Both involve low intrinsic growth rates of the bad phenotype compared to the internal rate of return. Critical thresholds may exist in such situations where mismanagement of genetic resources may lead to an increase in the frequency of a bad gene beyond a point where a permanently reduced frequency of the valuable gene, or even extinction, is optimal. 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 that directly affect survival, such as the ability to form groups to avoid predators or the size of individual animals. Further, mismanagement becomes more likely if selective harvesting substantially reduces the frequency of the preferred gene, either through a long period of selective harvesting or high selection pressures. In terms of the schooling behavior of pelagic fish, the dominance of the schooling strategy indicates that the survival rate of non-schooling individuals is significantly smaller in the absence of harvesting. Again, this implies that we find ourselves in a situation where it is initially optimal to reduce effort and conserve the good gene, but where critical thresholds exist beyond which a high frequency of the bad gene is optimal. Since current management practices may lead to a reduction in or even the extinction of valuable genes as the optimal policy, it is of great importance that managers of such resources reevaluate their management strategies. These results warn that simply assuming that all fish of a species are the same may lead to suboptimal management strategies that result in the extinction of valuable genes and the loss of resource rent to future generations.

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Appendix A. Glossary

The following definitions are slightly elaborated versions of definitions found in Ref. [8].

- **Allele:** One of the different forms of a gene at a gene locus on a chromosome.
- **Coefficient of selection:** A measure of the rate of transmission through successive generations of a given allele compared to the rate of transmission of another allele.
- **Genotype:** The genetic constitution of an organism, usually in respect to a single gene or a few genes relevant in a particular context. Two organisms of the same species are different genotypes with respect to a particular gene if the organisms have different alleles of that gene.
- **Mendelian genetics:** The scientific study of the role of genes in inheritance via sexual reproduction.
- **Phenotype:** The observable characteristics of an organism, dependent on genotype and environment. It may refer to its total physical appearance or to specific physical and/or behavioral traits. Two different genotypes may belong to the same phenotype if the different alleles do not give rise to differences in observable characteristics.
Appendix B. Derivation of the differential equation for $q$

This equation is a basic result in quantitative genetics. The exposition follows Ref. [9]. A gene is located at a locus. At any time $t$, if the fraction of genes at a particular locus that belongs to the allele $a$ is $q$, and the fraction belonging to the allele $A$ is $1–q$, then the population can be divided into three phenotypes. The fraction of the population being $aa$ is $Q_t = q^2$, the fraction being $Aa$ is $H_t = 2q(1–q)$, and the fraction being $AA$ is $P_t = (1–q)^2$. In the absence of any selection, the $q_{t+1}$ would be given by $q_{t+1} = (Q_t+1/2H_t)/(Q_t+H_t+P_t) = q_t$. If the aa individuals are uniformly selected against, this formula must be modified to take into account the new frequency of $q$.

$$q_{t+1} = \frac{(1–s)Q_t + (1/2)H_t}{(1–s)Q_t + H_t + P_t} = \frac{q_t – sq_t^2}{1–sq_t^2}. \tag{B.1}$$

Subtracting $q_t$ on both sides yields:

$$q_{t+1} – q_t = \frac{q_t – sq_t^2}{1–sq_t^2} – q_t = -s\frac{q_t^2(1–q_t)}{1–sq_t^2}. \tag{B.2}$$

This is a discrete time version of the differential equation for $q$ presented in Eq. (4). While differential equations and their corresponding difference equations can yield qualitatively different solutions when difference equation induces cyclic or chaotic behavior, this problem does not appear in the present case. Discrete time single-gene genetics does not exhibit cyclic or chaotic behavior except, possibly, for unrealistic parameter values. Thus, no qualitative types of solutions are lost when going from difference equations to differential equations.

Appendix C. Proof of Proposition 1

In the main text, a sufficient condition for the stability of a steady state $q_*$ is that $\Theta'(q_*)<0$. Conversely, a sufficient condition for the instability of $q_*$ is that $\Theta'(q_*)>0$. $\Theta'(q)$ is given by $\Theta'(q) = \Theta(H/\langle q \rangle_E = \langle A_q – B_q \rangle)$. To prove this, consider the following general optimal control problem:

$$\text{max } \int_0^\infty U(q, E) e^{-\delta t} dt \text{ s.t. } q = f(q, E), \text{ where } q(0) \text{ is given.} \tag{C.1}$$

Along the optimal path, $q = f(q, E(q))$. Here, $E(q)$ is the optimal choice of $E$ as a function of $q$. We denote $E(q^*)$ as $E^*$. In the present problem, $(\partial H/\langle q \rangle_E)_{q=E^*} = U_{E^*}(q, E^*) + \lambda f_{E^*}(q, E^*)$. The stability of $q^*$ holds if

$$\frac{d\Theta}{dq}\bigg|_{q=q^*} = \frac{\partial \Theta}{\partial q}\bigg|_{q=q^*} + \frac{\partial f}{\partial E}\bigg|_{q=q^*} \frac{dE}{dq}\bigg|_{q=q^*} < 0. \tag{C.2}$$

Here, $\delta$ indicates partial derivatives of the differential equation with respect to its argument. An expression for $dE/dq$ may be found by implicitly differentiating the first-order condition for $E$ and maximizing the Hamiltonian:

$$dE\bigg|_q = -U_{E^*}(q, E) + \frac{\partial f_{E^*}(q, E)}{\partial E} = -U_{E^*}(q, E) + \frac{\Theta'(q)}{\theta(q) + \lambda f_{E^*}(q, E)}. \tag{C.3}$$

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

References


