Biodiversity Economics

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20 Modelling the recolonisation of native species

Anders Skonhoft

1 Introduction

Recolonisation of native species typically represents an institutional change and reflects society's changing attitude to the species cost and benefit streams. When successful, recolonisation often influences the ecology and may come into conflict with existing economic activity. Such conflict may be particularly controversial and severe when the recolonised species are large carnivores, like wolves and grizzlies, which kill livestock and prey species with hunting and meat values. Recolonised animals may also induce conflicts with existing economic activities, like agriculture, including eating up crops and pastures and causing browsing damage. However, recolonised native species may also create hunting and trapping value or other types of consumptive values, in addition to non-consumptive values like existence value, tourist value and so forth (see Freeman 2003 for a general overview and Nunes and van den Bergh 2001 for a critical discussion of species valuation). In addition to ecology, these cost and benefit components and wildlife conflicts depend on the economic and institutional setting and there are obvious differences between, say, an East African region where people are located near wildlife with living conditions closely related to agricultural activities and, say, a region in Europe or North America where most people experience wildlife only through non-consumptive uses (Swanson 1994). The management goal will also generally differ. For these and other reasons it may seem difficult to formulate a general analytical model for studying economic impacts of species recolonisation. Nevertheless, this is actually what this chapter will attempt to do. Within such a general framework, however, several cases associated with specific economic and ecological circumstances will be considered. In the last part of the chapter, a more detailed example is studied.

Acknowledgements: Thanks to Anne B. Johannesen, Eric Naevdal, Jon Olaf Olaussen and one of the editors, Unai Pascual, for constructive criticism on an earlier draft of this chapter.

There is a difference between native recolonisation and reintroduction. While reintroduction is a man-made 'attempt to establish a species in an area which was once part of its historical range, but from which it has been extirpated or become extinct' (IUCN 1995, p. 2), recolonisation represents a species establishment in a historical habitat without *direct* man-made interventions. However, it seems difficult to make a clear-cut distinction as humans in many, if not all, instances, at least indirectly, influence recolonisations. This may typically occur when previous harvesting practices are banned, or when, say, previous production practices in agriculture and forestry influencing habitat conversion and species growth are changed. The recolonisation of the grey wolf (*Canis lupus*) in Scandinavia in the 1970s, to be considered below, is an example of recolonisation due to banning of previous harvesting practices. However, the difference between recolonisation (and reintroduction) and the existence of invasive species is clearer as invasive species represent an introduction of non-native species that generally alters an ecological system in a negative fashion and hence is an economic bad (Perrings 2007).

A recent well-known example of species reintroduction is the grey wolf in the Yellowstone National Park, North America. The first reintroduction took place in 1995 with a few wolves, followed by an additional reintroduction in 1996. The introduction was opposed by local ranchers who feared that wolves would prey on their livestock and by hunters who feared that wolves would compete with them for game. So far the wolf recovery seems to be a success story and the number of visitations to parts of the park where wolves are frequently seen has increased. However, some attacks on domestic sheep have been reported and the wolves have reduced the moose and bison population (e.g. Boyce 1997). The grey wolf has also recolonised Scandinavia during the last few decades (Wabakken *et al.* 2001). While small in number, this recolonisation has also caused several conflicts. Another example is the European bison (*Bison bonasus*) which now is found within its previous territory in Ukraine after its numbers dwindled as a result of overexploitation and agricultural expansion a long time ago. The reintroduction started in 1965 (Perzanowski *et al.* 2004) and so far the programme has resulted in eleven scattered herds, numbering about fifty animals. There seem to be few conflicts related to this reintroduction. Yet other examples are the translocations of the black-faced impala in Namibia which started in the early 1970s (Matson *et al.* 2004) and the lynx introduction in Steury and Murray (2004). In the journal *Biological Conservation*, several other recolonisations and reintroductions are reported, while Graham *et al.* (2005) provide a general overview of the various arising conflicts,

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In what follows, we basically examine species recolonisation. However, due to the somewhat unclear terminology and lack of precise definitions, the terms recolonisation and reintroduction will often be used synonymously. Previous economic analysis of recolonisation is scarce and only a few references are reported when using the term reintroduction in *Econlit* (no citations are reported when using the term recolonisation). A key paper is that of Rondeau (2001). He formulates an optimal control model aiming to analyse the reintroduction of a white-tailed deer population with numerical examples from the USA. In this work the shadow price of the reintroduced species may be either positive or negative, depending on the cost and benefit structure as well as the biological growth conditions. Rondeau's (2001) study hence has similarities with the recent bioeconomic literature where species may be valuable but also a pest (e.g. Huffaker *et al.* 1992; Zivin *et al.* 2000; Horan and Bulte 2004; Skonhoft and Schulz 2005), but it offers a more in-depth dynamic analysis than these other papers. One reason for this, which is a special feature of the Rondeau model, is that introduction of species is explicitly considered in the population growth model; that is, the stock may grow according to new species introduced from outside areas in addition to natural growth.

In contrast to Rondeau (2001), we consider an area with no further introduction. We are also looking away from possible dispersal, or migration, from outside areas. This approach is very similar to previous studies of the cost of invasive species (Perrings 2007) where the so-called *ex ante* net benefit (the scenario without invasive species) is compared with the *ex post* benefit (the scenario with invasive species). The various cost and benefit streams related to recolonised species, as experienced by different agents, or groups of people, will be considered within a unified management scheme. It is assumed that a benevolent social planner maximises the present-value social surplus. This can hence also include values experienced outside the given area that typically may include existence values. We continue this chapter with a formulation of a general bio-economic model of species recolonisation. In section 3, various special ecological and economic cases of this general model are considered. Then in section 4 one of these versions is analysed in more depth, focusing on the recolonisation of the grey wolf in Scandinavia. This section also contains a numerical illustration. The last section concludes with a summary of the main findings and gives some policy implications. The general conclusions are that some control of the recolonised species often pays off. However, recolonised species should be kept uncontrolled when they (i) do small damage, (ii) are expensive to control and (iii) prey upon existing species that cause various types of damage, like browsing or grazing damage. Based on the grey wolf example, a general conclusion is also that the effects of economic forces often are difficult to predict when operating in an interspecies relationship.

2 Ecological interaction and the various cost and benefit streams

Typically, recolonisation of a native species results from banning of previous hunting practices. In some instances, this reflects that an earlier considered pest species is recognised to carry positive non-consumptive values (viewing value, existence value and so forth). The above examples of recolonisation of large carnivores are of this type. At a later stage when the recolonised species has reached a 'sustainable' stock level, it may also be considered as valuable for harvesting, or trapping. Alternatively, if the actual species does not carry any harvesting value and it is socially desirable to control the species abundance, species control will incur costs. Depending on ecological, economic and institutional circumstances, recolonisation may also cause serious conflicts and damage to existing economic activities, like preying upon livestock (cf. the above examples). Similarly, in the case of the recolonised species being a grazer, the agricultural damage may include eating up crops and pastures. But damage can also be channelled through the ecological system with existing wildlife and may be of the predator–prey type, or of the competitive type. When the existing species has hunting, or trapping, value, this value is then potentially reduced through recolonisation. The wolf–moose example considered below is of this type. The already existing wildlife species may also have positive non-consumptive values, which potentially are reduced through the recolonisation as well. However, if the existing species cause grazing or browsing damage, reintroduced species may potentially reduce such damage, as will be shown with an example below.

We start by formulating the ecological sub-model. The population growth of the recolonised species, W, measured in biomass, or 'normalised' number of animals, is generally given as

$$dW/dt = G(W, X) - y \tag{1}$$

with $G(..)$ as the natural growth function and where one stock X (also measured in biomass) represents the existing wildlife affected by the recolonised species. Harvesting, y, is the control variable. As indicated, no dispersal term is included in equation (1) as we study situations where the recolonised species is established in the area and there is no further

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inflow from outside areas. In addition, and in contrast to Rondeau (2001), we assume $y \geq 0$, indicating that any direct man-made effort to reintroduce species is neglected as well. Accordingly, only natural growth in the given area together with possible control measures governs the population growth of the recolonised species. $\partial G/\partial X = G_X$ may be either positive (predator-prey relationship and where the reintroduced species is the predator) or negative (competitive relationship, or the reintroduced species is the prey). G_X can also be zero, or close to zero, which typically happens if the recolonised species is of the opportunistic type; that is, the food intake may be grass as well as different sources of meat. The brown bear (*Ursus arctos*) may fit this category, but also the grey wolf (see below). Finally, own density dependent growth G_W is generally assumed to be positive for a 'small' stock and negative for a 'large' stock. We further assume $G(0, X) = 0$ together with strict concavity, $G_{WW} < 0$.

The population growth of the existing species follows next as

$$dX/dt = F(X, W) - h \tag{2}$$

where $h \geq 0$ is the harvest, or trapping, and $F(..)$ the natural growth function. Also, $F_w < 0$ if the recolonised species competes with the existing wildlife or it is a predator–prey relationship and the recolonised species is the predator. If it is a prey, the effect will be the reverse and thus positive. However, this effect also may be weak, or even negligible. As above, F_X is typically positive for a 'small' stock size and negative for a 'large' stock size and also $F(0, W) = 0$ and strict concavity in own density, $F_{XX} < 0$, are assumed.

The current net benefit, or social surplus, is given as

$$\pi = H(y, W) + R(W) - S(W) + V(h, X) + Q(X) - D(X) \tag{3}$$

where $H(y, W)$ is the benefit of controlling the recolonised species while $V(h, X)$ is the net hunting, or trapping, value of the existing species, both terms generally depending on the number of animals removed together with the species abundance, $H_W \geq 0$ and $V_X \geq 0$. These values may be positive, negative or zero. For instance, $H(y, W) > 0$ when the harvesting value is substantial and the harvesting cost is small, while $H(y, W) < 0$ when the cost of removing the recolonised stock is substantial, accompanied by a small, or perhaps negligible, harvesting value.

Furthermore, as already indicated, the production activities practised within the given area interacting with the ecology typically depend on the species density and are of various categories (Table 20.1). First of all, $S(W) > 0$, with $S(0) = 0$, is the cost of, say, predation on livestock, or grazing damage of the recolonised species, with more species implying higher costs, $S' > 0$. $S(W)$ may therefore typically reflect the cost of

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Table 20.1 *Value categories*

Recolonised species			Existing species		
$H(y, W)$	$R(W)$	$S(W)$	$V(h, X)$	$Q(X)$	$D(X)$
Hunting/ trapping value	Positive stock value (existence value, viewing value, tourist value, etc.)	Negative stock value (grazing damage, livestock predation, etc.)	Hunting/ trapping value	Positive stock value (existence value, viewing value, tourist value, etc.)	Negative stock value (grazing and browsing damage, etc.)

livestock predation if the recolonised species is a large carnivore, while being grazing damage if it is a herbivore (Zivin *et al.* 2000). $R(W)$, with $R(0) = 0$, yields the existence value, viewing value, tourist value, etc. of the recolonised species and is also generally increasing in the number of animals, $R' > 0$, but the marginal benefit may be decreasing, $R'' < 0$ (Krutilla 1967). We next have the already existing species stock values, and where $D(X)$ is the potential damage cost, also supposed to increase in the species density, $D' > 0$ with $D(0) = 0$. This cost may represent browsing, or grazing, damage, such as moose causing forestry damage (see example below). The existing wildlife also generally carries a positive stock value $Q(X)$, like existence value, with $Q(0) = 0$. Also here we typically have $Q' > 0$ together with $Q'' \leq 0$.

When the social planner aims to maximise present-value net benefit, PV, the problem is to find harvest and control rates of the species that maximise

$$PV = \int_0^\infty [H(y, W) + R(W) - S(W) + V(h, X) + Q(X) - D(X)]e^{-\delta t}dt \tag{4}$$

subject to the ecological growth equations (1) and (2), together with the initial stock sizes and where $\delta \geq 0$ is the (social) discount rate assumed to be constant through time. The current value Hamiltonian of this problem reads

$$\Psi = H(y, W) + R(W) - S(W) + V(h, X) + Q(X) - D(X) + \mu[G(W, X) - y] + \lambda[F(X, W) - h] \tag{4a}$$

with y and h as control variables, W and X as state variables and λ and μ as the shadow values of the existing species and the recolonised species,

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$$\partial\Psi/\partial y = H_y(y, W) - \mu$$
$$\partial\Psi/\partial h = V_h(h, X) - \lambda \leq$$
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respectively. It follows that the conditions (5–8) yield the necessary conditions for a maximum when it is socially desirable to keep both species and when any upper binding constraints on the control variables are neglected.

$$\partial\Psi/\partial y = H_y(y, W) - \mu \leq 0; \quad y \geq 0 \tag{5}$$

$$\partial\Psi/\partial h = V_h(h, X) - \lambda \leq 0; \quad h \geq 0 \tag{6}$$

$$\begin{aligned} d\mu/dt = \delta\mu - \partial\Psi/\partial W = \delta\mu - H_W(y, W) - R'(W) + S'(W) \\ - \mu G_W(W, X) - \lambda F_W(X, W) \end{aligned} \tag{7}$$

$$\begin{aligned} d\lambda/dt = \delta\lambda - \partial\Psi/\partial X = \delta\lambda - V_X(h, X) - Q'(X) + D'(X) \\ - \mu G_X(W, X) - \lambda F_X(X, W) \end{aligned} \tag{8}$$

The control condition (5) holds as an equality if it is optimal with control, $y > 0$, of the recolonised species along the optimal trajectory. The marginal net harvesting benefit should then be equal to the species' shadow value. Otherwise, with $y = 0$, it will be inequality. If it is optimal with no harvest of the existing species, condition (6) also holds as an inequality. In both instances of zero harvesting, the marginal benefit of control, positive or negative, should be below that of the shadow price, which may be positive or negative as well (more details below). The portfolio conditions (7) and (8) reflect the evolution of the shadow price of the recolonised species and the existing species, respectively. Dividing with μ, condition (7) is the recolonised species Hotelling efficiency rule, indicating that the growth rate of the shadow price should be equal to the external rate of return as given by the discount rent δ, minus the internal rate of return. Condition (8) has a similar interpretation for the existing species.

The shadow prices may be eliminated from the above system (5)–(8) and the reduced form solution together with the ecological growth equations (1) and (2) yield, in principle, a set of four interconnected differential equations between the two control variables, y and h, and the two state variables, W and X. However, it is not possible to say very much about the dynamics, or the steady state, of this system without further specification of the functional forms and without stating whether the ecological interaction is of the competitive or predator-prey type. Even then, the system will typically be too complex – see, for example, the much simpler two-species model in Ragozin and Brown (1985) where the predator alone is subject to harvest and there are no stock values. We therefore proceed to look at some simplified cases.

3 Simplified cases

Not surprisingly, loosening up the interaction between reintroduced and existing species results in more tractable situations to analyse. The same occurs if the net benefit functions of species control are given a more specific content. Altogether, four special cases are considered. First, two cases assuming negligible ecological interaction are studied. Then, two other cases are analysed with simplified harvesting functions.

3.1 *The case of negligible ecological interaction*

In many instances, the interaction between recolonised species and existing species is weak, or even negligible. The above example of the European bison is of this type and this may also be so when the recolonised species is of the opportunistic type (like the brown bear). The natural growth functions of the recolonised species and the existing species (1) and (2) reduce then to $G(W)$ and $F(X)$, respectively. As a consequence, there will be no economic interdependency between the species as well and the recolonised species can be managed separately from the existing one. Therefore, conditions (5) and (7a) yield the optimality conditions for the recolonised species together with $dW/dt = G(W) - y$.

$$d\mu/dt = \delta\mu - H_W(y, W) - R'(W) + S'(W) - \mu G'(W) \qquad (7a)$$

As the harvesting value may be either positive or negative and various stock values are included, this is very similar to the models considered by Horan and Bulte (2004), Skonhoft and Schulz (2005) and others. As demonstrated in these models, the shadow price, μ, may be positive or negative. It will be positive if harvesting is profitable, while it is negative when controlling is a costly activity mainly for damage control. The ambiguous sign of the shadow price can result in a non-convex Hamiltonian together with possible multiple equilibria (see also Rondeau 2001 and Dasgupta and Mäler 2003). Obviously, we find the shadow price to be negative if the recolonised species (when controllable, see below) carries no trapping or hunting value, but demand effort to be controlled. It may, however, even be negative with a positive harvesting value if it, on the margin, is more costly to control the species so that $H_y(y, W)$ is negative at the optimum. Horan and Bulte (2004) analyse the dynamics of this model. When a non-linear control benefit function $H(y, W)$ is applied, they find, not surprisingly, the steady state(s) to be of the saddle point type.

When it is optimal to steer the system towards the steady state(s), condition (5) as an equity combined with (7a) gives the golden-rule condition:

$$\begin{aligned} &G'(W) + H_W(y, W)/H_y(y, W) \\ &\quad + [R'(W) - S'(W)]/H_y(y, W) = \delta \end{aligned} \qquad (9)$$

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The left-hand side of (9) yields the internal rate of species return at the optimum, which should be equal to the external rate as given by the discount rent δ. This condition together with the species growth condition (1) in equilibrium determine the steady states for W^* and y^*. If the shadow price is positive and there is a positive net harvesting benefit, $H_y > 0$, and the negative stock value dominates the positive one, $(S' - R') > 0$, it is seen that it is optimal to keep a small density of the recolonised species. If the shadow value is negative and the species may be classified as a pest, we reach the opposite conclusion. The comparative static results may also be ambiguous and typically we find that a higher rate of discount yields a higher steady-state stock W^* when the shadow price is negative, which is the opposite of the standard harvesting model (Clark 1990). See also Skonhoft and Schulz (2005).

3.2 *The case of a fixed shadow price of the recolonised species together with negligible interaction with the existing species*

Often it may be reasonable to assume that the control cost of terrestrial animal species is density independent. This typically occurs under a hunting licence scheme (see below). If additionally the net harvesting benefit, positive or negative, is linear in the amount of animals controlled, or harvested, condition (5) indicates a constant shadow price when it is beneficial to control the species along the optimal trajectory. When still assuming a negligible ecological interaction, the recolonised species portfolio equation (7a) reduces to

$$0 = \mu\delta - R'(W) + S'(W) - \mu G'(W) \qquad (7b)$$

Equation (7b) is a static one because the Hamiltonian now is linear in the control y and the dynamics leading to the steady state will be of the Most Rapid Approach Path (*MRAP* dynamics, see, for example, Clark 1990). The golden rule condition (7b) also indicates that the internal rate of return, now as $G' + [R' - S']/\mu$, should be equal to the external rate, δ. Another interpretation is that the net marginal value of the species 'in the forest', $(\mu G' + R' - S')$, should be equal to the marginal harvesting value 'in the bank', $\mu\delta$.

If $\mu^* > 0$, condition (7b) represents the solution of the standard one-species harvesting model missing the usual stock-dependent cost term, but extended with positive as well as negative stock values. Depending on their marginal values, the optimal number of species W^* can be below or above that of the maximum sustainable yield level, W_{msy}. If it is costly to control and $\mu^* < 0$, we find that the optimal managed stock will be smaller when a nuisance effect is linked to it than without this effect. Therefore, reintroduced species will be left uncontrolled if they have no negative effect and are costly to control.

An even more simplified situation emerges if the harvesting benefit is small or negligible, i.e. $H(y, W) = 0$. As the marginal harvesting income is also zero, $H_y = 0$, $\mu^* = 0$ when it is still beneficial to control the species. Condition (7b) reduces then further to $-R'(W) + S'(W) = 0$ and the socially desirable number of species W^* is simply determined by the equalisation of the marginal values.[1] While the optimal species number is invariant of natural growth, the steady-state harvest follows from the population growth equilibrium $G(W^*) = y^*$. The same conclusion may be reached when the existing species influences the growth of recolonised species, thus with $G(W, X)$. Of course, in this case the level of the control y^* will differ.

In case it is socially desirable not to control, or harvest, the species along the optimal trajectory, condition (5) yields $\mu > 0$ when $H_y = 0$. The number of recolonised species would then approach its carrying capacity in the long term. From condition (7b), $\mu^* = (R' - S')/(\delta - G')$ is the shadow price of the unexploited stock. Because G is a humped function with $G' < 0$ in the unexploited situation (section 2 above), $(R' - S') > 0$ must hold to ensure a positive shadow value. Thus, not surprisingly, it is optimal to leave the species uncontrolled because the marginal positive stock value exceeds the negative one. Under these conditions it is also seen that reintroduced species unambiguously will be left uncontrolled if they have no negative effect.

3.3 *The case of ecological interaction without harvesting benefit of the recolonised species*

For various reasons, the harvesting profit of the recolonised species may be zero, or close to zero. This may happen if, say, the harvesting benefit is small and negligible and the control cost is small and negligible as well (see the wolf example below). When $H(y, W) = 0$, $\mu = 0$ still holds if it pays to control along the optimal trajectory. When there is ecological interaction, the portfolio conditions yield

$$0 = -R'(W) + S'(W) - \lambda F_W(X, W) \tag{7c}$$

and

$$d\lambda/dt = \delta\lambda - V_X(h, X) - Q'(X) + D'(X) - \lambda F_X(X, W) \tag{8a}$$

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[1] Concavity of the Hamiltonian requires in this case that $R'' - S'' < 0$ (c.f. section 4).

The portfolio condition (7c) of the re
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3.4 *The case of ecological interac recolonised species and with existing species*

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that $R'' - S'' < 0$ (c.f. section 4).

The portfolio condition (7c) of the recolonised species is also now a static equation and it can be noted that the opportunity cost of the recolonised species' biological capital is zero as the discount rent δ is not included. The optimal number of animals is found where the marginal stock value $R'(W)$ is equal to its marginal cost, comprising the damage cost, $S'(W)$, and the cost of predation evaluated at the existing species shadow value, $\lambda F_W(X, W)$.

To solve this system, the shadow price of the existing species, λ, may in a first stage be eliminated from equation (7c) and (8a) by using the control condition (6) which holds as $\lambda = V_h(h, X)$ when harvest of the existing species takes place along the optimal trajectory. W can be expressed as a function of X and h through equation (7c). In a next step, W may be substituted away from (8a). The reduced-form dynamic system is consequently steered by equation (8a) together with the population growth equation (2), comprising the variables X and h. The dynamics of this system may be quite similar to the first case with no ecological interaction between the species, thus yielding the possibility of multiple equilibria for the recolonised species. At the steady state, it can be shown that $R'(W^*) - S'(W^*) > 0$ if $\lambda^* > 0$ and the recolonised species prey upon, or compete, with the existing species (i.e. $F_W < 0$). The opposite holds if the existing species turns out to be a pest and $\lambda^* < 0$.

3.4 *The case of ecological interaction without harvesting benefit of the recolonised species and with a constant harvesting value of the existing species*

In some instances the harvesting value of the existing species may simply be given by the meat value, or net hunting price p. Therefore, the harvesting value becomes $V(X, h) = ph$ and condition (6) reduces to $p = \lambda$ if it is profitable to harvest. If condition $H(y, W) = 0$ with $\mu = 0$ holds and it is still beneficial to control the recolonised species along the optimal trajectory as well, it turns out that

$$0 = -R'(W) + S'(W) - pF_W(X, W) \tag{7d}$$

and

$$0 = \delta p - Q'(X) + D'(X) - pF_X(X, W) \tag{8b}$$

This is a double singular system with dynamics of the *MRAP* type, or close to *MRAP* (see Clark 1990). While the natural growth of the existing species still influences the outcome, the recolonised species' natural growth does not because of the assumption that harvesting has zero profit and $\mu = 0$. If the recolonised species prey upon, or compete, with the existing species, $R'(W^*) - S'(W^*) > 0$ holds unambiguously at the steady-state equilibrium. Not surprisingly, a higher positive marginal species value yields a higher optimal stock while more damage works in the opposite direction. Even in this simplified model, however, other comparative static results are far from clear and a higher harvesting price, p, may either increase or reduce the optimal number of recolonised species. The stock effects of a higher discount rate δ are generally unclear as well. These results are examined in more detail in the example of the recolonisation of the grey wolf in Scandinavia which includes a wolf–moose (*Alces alces*) ecological interaction.

4 The recolonisation of the Scandinavian wolf

In the mid-1960s, the grey wolf was regarded as functionally extinct in Norway and Sweden (the Scandinavian Peninsula). However, due to banning of earlier hunting practices it recolonised and in the latter part of the 1970s the first confirmed reproduction in fourteen years was recorded. Since this first reproduction in Northern Sweden, all new reproductions have been located in South-central parts of the Scandinavian Peninsula. The recolonised wolf population in Scandinavia now numbers some 100–120 individuals which live in small family groups, or packs, in the Western-central part of Sweden and along the border area between Norway and Sweden (Wabakken *et al.* 2001).

Although the wolf population is still numerically small, its recolonisation is already associated with several conflicts. One is due to predation on livestock, including sheep and reindeer. Although the total loss is modest, some farmers in a few areas have been seriously affected, as in the abovementioned example from Yellowstone. In addition, predation on wild ungulates is another conflict, especially where the wolf shows a particularly strong preference for moose. As a consequence, a smaller moose population is available for hunting. In fact, while the problem of moose predation also takes place in only a few areas, it has caused great concern in rural Scandinavia because moose is by far the most important hunting game species, with about 40,000 and 100,000 animals (with a mean body weight of about 190 kg for adult females and 240 kg for adult males) shot every year in Norway and Sweden, respectively. In addition, moose hunting in September/October is an important, if not the most important, social and cultural event in many rural communities (Skonhoft 2006).

Moose–wolf ecology has been subject to several intensive studies, mostly in North America. From these studies it appears clear that wolves, when present, influence the abundance of moose (Peterson 1999). The

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Scandinavian ecosystem, however, differs from the North American system as the moose density is generally higher. Additionally, the age and sex structures differ because of selective hunting schemes with a higher-proportion harvesting of calves and young males. Another important difference is that in Scandinavia harvesting accounts for a greater share of total mortality. Last but not least, wolf density in Scandinavia is also significantly lower and more patchily distributed (Wabakken *et al.* 2001). It thus follows that the moose–wolf ratio is higher in Scandinavia and the impact of wolf predation is likely to be of a more local nature. Wolf predation is focused on calves, yearlings and older females, with calves as the main food source. The predation rates reported from Scandinavia also appear to be higher than those in North America, which may indicate that predation, for a given size of wolf pack, increases with moose density (Nilsen *et al.* 2005).

Based on the studies cited above, it can be assumed that wolf predation represents an additional source of mortality for calves, yearlings and older females. In our biomass framework, the wolf population then negatively affects the natural growth of the moose population. It is assumed that the predation increases with the size and number of the wolf packs as well as the size of the moose stock. There may also be a feedback effect as the size of the moose population influences wolf population growth. However, in areas with colonising carnivore populations, this relationship will appear less interactive, meaning that the wolves are not able to respond numerically to variations in the moose population (Nilsen *et al.* 2005). Any numerical response of the wolf population is hence neglected. The ecological model of the wolf–moose interaction is therefore described by equation (2) $dX/dt = F(X, W) - h$, while equation (1) again reduces to $dW/dt = G(W) - y$.

We then have the cost and benefit streams of the considered system and we start with the wolf stock values. The livestock predation cost on sheep and reindeer of the wolf $S(W)$ is suspected to be quite small, but, as indicated, it can be of significance in a few areas (Milner *et al.* 2005). Yet the non-consumptive wolf stock value (including the intrinsic value and viewing value), $R(W)$, is suspected to be high (Boman and Bostedt 1999). However, as the stock value is highly uncertain, the effects of different assumptions need to be studied. It may be costly to control the wolf population, or it may be controlled by selling hunting licences. Another possibility is that the controlling costs more or less cover the benefits so that the net harvesting value may be small or negligible. All these possibilities are explored next when assuming that the harvesting income, or cost, increases linearly in the number of controlled animals while neglecting any stock effect.

Landowners obtain the hunting profit of the moose. The yearly hunting income is given as $V(h, X) = ph$, with p as the net hunting licence price, assumed to be fixed and independent of the harvest and stock size. This is justified by the fact that there is competition among a large number of suppliers of hunting licences in Scandinavia. Following the practice in Norway (and Sweden), one licence allows the buyer to kill one animal, which is paid only if the animal is killed. The moose population also causes browsing damage to landowners, the damage on young pine being of particular importance (Wam *et al.* 2005). The damage on young pine occurs basically during the winter and varies with the quality of the timber stand and the productivity of the forest. The damage may take place immediately and damaged young pine trees may be replaced directly, but quite frequently there is a time lag between the occurrence of browsing and the economic loss of the damage. In such instances, however, discounting is not taken into account explicitly. There are also other costs connected to the moose population, the single most important being related to moose–vehicle collisions. This cost is considerable and recent estimates indicate that it may be even higher than the meat value of the moose (Skonhoft 2006). Thus, the damage cost function of the moose, $D(X)$, covers grazing damage as well as the cost of traffic collisions. There will also be a positive stock value of the moose population (viewing value, etc.). However, because of the large number of moose in Scandinavia, $Q(X)$ is suspected to be quite small, if not negligible, at the margin.

The wolf–moose example is a mix between the second and fourth cases introduced in the introduction. That is, (i) there is only a one-way ecological interaction, (ii) there is a fixed control value of the recolonised species (positive, negative or zero), and iii) the harvesting value of the existing species is not stock dependent and is linear in the amount harvested. The shadow value of the recolonised species will be constant when assuming that the wolf population is controlled along the optimal trajectory all the time. It follows that $H_y = \mu$ which is positive, negative or zero, while the control condition (6) of the existing species, the moose, is $p = \lambda$ when harvesting pays off. The dynamics of this system will therefore obey an *MRAP* path and the reduced-form steady state is given by

$$0 = \mu\delta - R'(W) + S'(W) - \mu G'(W) - pF_W(X, W) \qquad (10)$$

and

$$0 = p\delta - Q'(X) + D'(X) - pF_X(X, W) \qquad (11)$$

These two equations determine X^* and W^* simultaneously. In a next step, the number of animals removed can be derived from the equilibrium

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$$p\alpha X + (2\mu\gamma/L + r_2)W =$$

and

$$(2p\beta/K)X + p\alpha W = p($$

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population growth conditions. The wolf population may be above or below that of the maximum sustainable yield level, W_{msy}, and this may also occur for the moose population. The comparative statics are also generally unclear and a higher harvesting price of the moose may either increase or decrease the socially desirable number of moose. For this reason, the wolf stock effect will be unclear as well. The effect of a higher discount rate is suspected to influence the wolf stock negatively, but this effect is also unclear because it affects the population directly as well as indirectly through the moose population equilibrium condition (11).

To shed further light on the economic and ecological forces at work, the functional forms of the various functions need to be specified. The wolf stock growth is assumed to be logistic, $G(W) = \gamma W(1 - W/L)$, with γ as the maximum specific growth rate and L as its carrying capacity. Similarly, the natural growth of the moose population in the absence of wolf predation is assumed to be of the standard logistic type, while the predation effect (the functional response) is specified in a Cobb-Douglas manner, $F(X, W) = \beta X(1 - X/K) - \alpha WX$, where $\alpha > 0$ is the predation coefficient. Therefore, the functional response of the moose population implies a fixed predation rate (as a growth rate), αW, and indicates that the amount of predation increases linearly with the size of the moose stock.

For simplicity, it is assumed that the moose stock values are linearly increasing in stock size. Therefore, for the moose population, we have $D(X) = dX$, with $d > 0$ as the constant damage cost per moose, including browsing damage as well as traffic damage, and $Q(X) = qX$ with $q > 0$ as the fixed positive moose stock value. For the wolf population, we also assume a linear damage function with constant damage cost per wolf, $S(W) = sW$ with $s > 0$. However, quite realistically, a strictly concave function is imposed for the wolf intrinsic value. This may secure a meaningful solution of the optimisation problem even if the recolonised species shadow value is negative (see below) and the function is specified as $R(W) = r_1 W - (r_2/2) W^2$. The value of the parameters $r_1 > 0$ and $r_2 > 0$ are scaled such that the marginal value all the time is positive.[2] Inserted into the above conditions (10) and (11) it follows that

$$p\alpha X + (2\mu\gamma/L + r_2)W = \mu(\gamma - \delta) + (r_1 - s) \qquad (10a)$$

and

$$(2p\beta/K)X + p\alpha W = p(\beta - \delta) + (q - d). \qquad (11a)$$

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[2] Typically, the moose positive stock value $Q(X)$ is suspected to be strictly concave as well. However, for simplicity, it is given as a linear function as this has no influence on the qualitative structure of the solution.

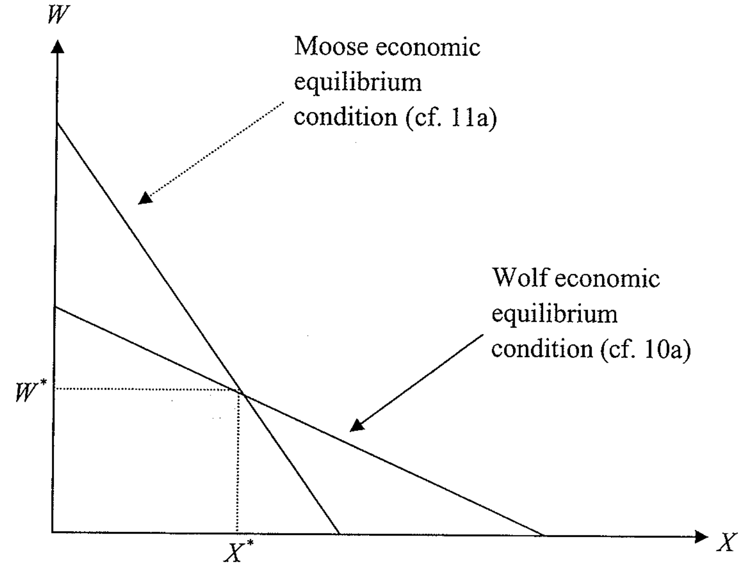

Figure 20.1. Wolf–moose economic equilibrium

These equations are straight lines in the X, W plane. The moose equilibrium condition (11a) slopes unambiguously downwards while the wolf equilibrium condition (10a) may slope downwards as well as upwards depending on the sign and size of the shadow value. However, due to the second-order conditions for a maximum, it must slope downwards but be less negatively sloped than the moose equilibrium condition (Figure 20.1). Two parameters are of particular importance here: the ecological interaction coefficient, α, in addition to the shadow value μ. Hence, to obtain a meaningful solution of the maximum problem, the predation pressure cannot be too strong while the shadow price, if negative, cannot be too largely negative.[3]

Table 20.2 reports the comparative static results. The effects of shifts in the stock values are straightforward. If, say, the positive wolf stock

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[3] The Hamiltonian must be jointly concave in the control and state variables to fulfil the second-order conditions for maximum. It can be demonstrated that this requires $\Omega = (2p\beta/K)(2\mu\gamma/L + r_2) - (p\alpha)^2 > 0$ together with $-(2\mu\gamma/L + r_2) < 0$. Ω is the determinant of the left-hand side of equations (10a) and (11a), and $\Omega > 0$ indicates that equation (11a) should be more negatively sloped than equation (10a). There must also be various restrictions on the parameter values to obtain an interior solution with positive stock sizes and stock sizes below its carrying capacities. The moose equilibrium condition (11a) must hence intersect at the W axis above that of the wolf equilibrium condition (10a) while (10a) must intersect with the X axis outside that of equation (11a). For a related discussion, see Skonhoft (1995).

Table 20.2 *Wolf recolonisatio
comparative static results*

	r_1	d	p
W^*	+	+	+/(−)
X^*	−	−	−/(+)

value, r_1, increases permanently,
wolf population. As a result, the
the number of moose will be reduc
cost, d, increases due to, for inst
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It is difficult (if not meanin
songbird?') to try to calculate th
monetarily as it comprises, an

Table 20.2 *Wolf recolonisation example – comparative static results*

	r_1	d	p	μ	δ	α
W^*	+	+	+/(−)	−/+	−/(+)	−/(+)
X^*	−	−	−/(+)	+/−	−/(+)	−/(+)

value, r_1, increases permanently, the social planner will keep a larger wolf population. As a result, the predation pressure will increase and the number of moose will be reduced accordingly. If the moose damage cost, d, increases due to, for instance, a higher frequency of moose–vehicle collisions, it will also be beneficial given a higher wolf population to increase the predation pressure and reduce the number of moose and hence the damage. Interestingly, the effects of a permanently higher rate of discount are generally unclear. However, if the wolf shadow price is positive, it can be shown that at least one of the stocks will decrease if δ increases. The effects of a more valuable moose harvest are ambiguous as well. On the one hand, a higher p will increase the moose number for a given size of the recolonised wolf population. This is because the marginal damage dominates the marginal positive stock value. Therefore, the relative damage cost will be reduced. This effect will be reinforced as the cost of predation increases and the wolf equilibrium line (10a) shifts inwards. On the other hand, if the marginal moose damage is small and negligible and is dominated by the positive stock value, no clear conclusion can be drawn. In either case, the effect on the wolf number will be the opposite.

The effects of a shift in the wolf shadow value are also ambiguous. If the shadow value is positive and increases, the result will be a smaller wolf population, suggesting that the net marginal stock value $(r_1 - s)$ is positive. The predation pressure hence reduces and the moose population increases accordingly. But if $\mu < 0$ and the control cost increases further, it will be beneficial with a higher wolf population, again under the reasonable assumption that the positive marginal stock value dominates the negative one. If the shadow price is zero, (10a) simply reads $W = (r_1 - s)/r_2 - (p\alpha/r_2)X$. The effects of a higher predation pressure through α are also generally unclear. However, it can be shown that at least one of the stocks will decrease.

It is difficult (if not meaningless; 'what is the money value of a songbird?') to try to calculate the stock value of the recolonised species monetarily as it comprises, among others, its existence value. It is, however, possible to reveal this value indirectly by imposing a quantitative restriction on the number of reintroduced wolves. To make things simple, while capturing the main points, any net harvesting benefit is neglected so the shadow value is zero, $\mu = 0$. In addition, the wolf damage cost together with the moose existence value are assumed to be small and negligible as well, i.e. $s = 0$ and $q = 0$. It thus follows that conditions (10a) and (11a) reduce to $p\alpha X + r_2 W = r_1$ and $(2p\beta/K)X + p\alpha W = p(\beta - \delta) - d$, respectively. Therefore, for a wolf target level $\bar{W}$, the marginal stock value reads as follows:

$$r_1 = \frac{K\alpha}{2\beta}[p(\beta - \delta) - d] + \frac{K}{2p\beta}\left[\frac{2p\beta r_2}{K} - (p\alpha)^2\right]\bar{W} \qquad (12)$$

The calculation is illustrated by using data from the Koppang area, some 300 km north of Oslo. A wolf pack settled in this region in 1997 in an area of 600 km^2, with a moose population of about 1000 individuals. Since then the number of wolves has been between five and twelve (more details are provided in Skonhoft 2006). A target level of ten wolves illustrates the calculations, $\bar{W} = 10$. The following parameter values are used. The moose carrying capacity is $K = 3,500$ (number of moose) which implies about 5.8 moose per square km. The moose maximum specific growth rate is $\beta = 0.47$, while the predation coefficient is assumed to be $\alpha = 0.005$ (1/wolf). The hunting licence price is $p = 8$ (1000 NOK/moose, 2003 prices), the marginal damage cost is $d = 1$ (1000 NOK/moose, 2003 prices) and the discount rent is $\delta = 0.05$. Finally, the baseline changing marginal wolf stock value is assumed to be $r_2 = 10$ (1000 NOK/wolf^2).

For these parameter values, we find $r_1 = 137$ (1000 NOK/wolf), indicating the value $R = r_1 \bar{W} - (r_2/2)\bar{W}^2 = 865$ (1000 NOK) and the marginal value $R' = r_1 - r_2 \bar{W} = 37$. Consequently, on these premises, the stock value of the target level wolf pack of $\bar{W} = 10$ must be at least 865 if recolonisation should be beneficial from a social point of view. Not surprisingly, r_1 and hence R decrease if the damage cost of the moose population increases, while r_1 increases when the moose hunting becomes more valuable. If, say, the hunting value p is doubled, we find $r_1 = 192$, while doubling the marginal damage d yields $r_1 = 118$.[4]

Altogether, these calculations indicate that, depending on cost and price assumptions, the break-even wolf stock value may vary widely. Nevertheless, the calculations demonstrate a quite modest wolf value to justify recolonisation. If the moose browsing and traffic damage increase, the critical marginal recolonisation value decreases as the predation then

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[4] If instead supposing that the marginal stock value reduces more slowly with $r_2 = 5$, while the other parameters are left unchanged, we find $r_1 = 86$ and $R = 615$. With $r_2 = 20$, meanwhile, the result is $r_1 = 236$ and $R = 1365$.

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5 Conclusion

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5 Conclusion

Species recolonisation typically takes place in an environment where earlier harvesting practices are banned, or when previous production practices in agriculture and forestry influencing habitat conversion and species growth are changed. Therefore, recolonisation often represents an institutional change and reflects society's changing attitude to the species cost and benefit streams. When successful, recolonisation often influences existing ecology and may come into conflict with existing economic activities. However, it may also create hunting and trapping value in addition to non-consumptive values like existence and viewing value. Ecology and institutions shape these costs and benefit streams experienced by different agents and groups of people.

Correctly modelling the key interspecies relationship is the critical part of studying the economic effects of recolonised species and various situations have been considered in this chapter. Using a general model in which recolonised species interact with already existing species, like a traditional predator–prey interaction, it becomes apparent that it is difficult to explain the dynamics and also the economic and ecological forces forming the equilibrium that eventually settles. Therefore, in order to shed additional light, at the cost of generality, some simplified cases have been proposed. Not surprisingly, loosening up the interaction between reintroduced and existing species yields more traceable situations to analyse. However, even in such cases, the economic and ecological forces at work are often difficult to assess.

The general insight from these models is that some control of the recolonised species often pays off. However, recolonised species should be kept uncontrolled when they (i) do small damage, (ii) are expensive to control and (iii) prey upon existing species that cause various types of damage, like browsing or grazing damage. A calibrated example of the recent experience of the recolonisation of the grey wolf in Scandinavia sheds further light on the various ecological and economic mechanisms working. This example demonstrates that the wolf value may be quite modest to justify the wolf recolonisation. This example also demonstrates that the effects of economic forces often are difficult to predict when operating in an interspecies relationship. This indicates that detailed knowledge about the ecology and cost and benefit structure is crucial to carry out a sound recolonised species management policy.

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