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Analysis

# The Optimal Timing of Reintroducing Captive Populations Into the Wild

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ABSTRACT

We examine a conservation problem in which the recovery of an endangered species depends on a captive breeding and reintroduction program. The model is applied to the case of the black-footed ferret (*Mustela nigripes*), an endangered species in North America reliant on captive breeding for survival. The timing of reintroduction is an important concern in these programs as there is a tradeoff between the duration (and therefore the cost) of the captive breeding program and the period the population spends in recovery and in the wild. In this paper, we develop a stylized bioeconomic model to determine the optimal reintroduction time, in which the objective is to minimize the cost of reintroduction while providing a viably-sized population in the wild. Our control variable is the timing of reintroduction, which departs from a large body of work in bioeconomics that focuses on adjustable controls that directly affect the target population. Generally, we find it is optimal to reintroduce ferrets early in a reintroduction program, although this result is contingent on species interactions and provisioning services.

## 1. Introduction

Wildlife translocation and reintroduction is a popular but costly conservation tool. Over the last few decades, several hundred reintroduction programs have augmented existing or reestablished extirpated wildlife populations (Wolf et al., 1996; Griffiths and Pavajeau, 2008; Godefroid et al., 2011). However, these programs are frequently criticized as expensive and ineffective (Ricciardi and Simberloff, 2009; Kleiman et al., 1994). Translocation typically follows a period of captive breeding, which requires substantial investments in facilities, fodder and genetic diversity maintenance.

This paper analyzes the optimal timing of translocation while accounting for the costs of managing captive and wild populations. We develop a bioeconomic model of captive rearing and reintroduction, including a wild prey population for the reintroduced individuals. We then use this model to determine the reintroduction time that minimizes total management costs, which include post-reintroduction costs associated with disease management, among other economic values. In doing so we re-derive the optimality conditions for a time optimal control problem, modeling a coupled predator-prey system in which the dynamics are endogenously linked at the reintroduction time. If the management objective is to minimize the costs of reintroduction subject to providing a viable long-term population in the wild, then a manager must consider the direct financial costs of managing the species in question, plus any indirect costs and benefits generated by the reintroduced species.

Existing studies of reintroduction programs tend to focus on post-reintroduction outcomes. Population viability analyses are commonly used to account for stochastic events and identify minimum viable populations for endangered species (Beissinger and Westphal, 1998; Morris and Doak, 2002). However, these analyses abstract from economic considerations. For black-footed ferrets, research has also focused on the influence of age structure (Klebanoff et al., 1991), habitat heterogeneity and space (Bevers et al., 1997), disease (Shoemaker et al., 2014), and uncertainty (Seal et al., 1989) in preparing for reintroductions. Thus, there is a critical need for research that incorporates economics into reintroduction problems.

Bioeconomic models that integrate economic and biophysical components are often used to show that failure to consider relevant costs and benefits in resource conservation leads to inefficient outcomes (Clark, 1973; Clark and Munro, 1976; Clark and Kirkwood, 1986; Wilen and Brown, 1986; Mesterton-Gibbons, 1987, 1988; Crocker and

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Tschirhart, 1992; Brock and Xepapadeus, 2002). Among other topics, these models have been used to analyze fisheries (Gordon, 1954; Hilborn, 1976; Sanchirico and Wilen, 1999), biological invasions (Leung et al., 2002; Horan and Fenichel, 2007; Fenichel et al., 2010; Epanchin-Niell and Hastings, 2010; Homans and Horie, 2011), and endangered species (Alexander, 2000; Melstrom and Horan, 2014). Several bioeconomic papers on the subject of endangered species examine reintroduction problems. Rondeau (2001) was among the first to examine the management of a reintroduced population with a bioeconomic model, while Horan and Melstrom (2011) include the possibility of reintroducing captive animals if the wild population goes extinct. Canessa et al. (2015) examine the issue of reintroduction under uncertainty.

This paper advances bioeconomic research by explicitly examining the timing of translocation for captive breeding and reintroduction programs. We build on prior work by analyzing a cost minimization problem in which time, rather than a stock or harvest variable, is the control. Very few studies consider time as the control (Hartwick et al., 1986; Conrad, 1999; Holland and Moore, 2003; Amit, 1986). Although conceptually similar, the classic Faustmann rotation problem and its extensions consider a single period of net benefits in the optimization process (Conrad, 1999; Newman et al., 1985; Loisel, 2011; Olschewski and Benitez, 2010; van Kooten et al., 1995). This is in contrast with our problem, in which benefits or costs accrue before and after reintroduction. Amit (1986) derives the optimal time to switch between primary and secondary methods of petroleum extraction. Hartwick et al. (1986) and Holland and Moore (2003) consider the optimal timing of switching between (non)renewable resources. However, we believe that the complexity of the ecology of species reintroductions makes a direct application of their methods unsuitable. We model two renewable resources coupled as a predator-prey system, where the dynamics of each resource not only change pre- and post- reintroduction but are also endogenously linked at the reintroduction time. Managers control the system only though the choice of reintroduction time. Following a general first-principles approach applied by Conrad and Clark (1987) for optimal harvest, we re-derive the conditions for optimality for a time optimal control problem. Researchers may therefore find the methods in this paper useful in solving other endogenous time problems.

We apply our model to the reintroduction of the black-footed ferret (*Mustela nigripes*), one of the flagship species for reintroduction in North America. Originally prevalent across the Great Plains, mountain basins, and semi-arid grasslands of North America, the black-footed ferret became an endangered species as a result of the sharp decline in its primary food source, prairie dogs, due to habitat conversion, disease, and poisoning (Miller et al., 1996). The ferret recovery strategy combines captive breeding and reintroduction to achieve a population level that no longer warrants a listing under the U.S. Endangered Species Act (ESA). Currently it is estimated that there is a minimum of 418 adult, breeding individuals among 11 reintroduction sites, with another 280 individuals in captivity (USFWS, 2013).

The main contribution of this paper is the methodology of incorporating economics into reintroduction problems, the use of time as a control, and the modeling of a coupled predator-prey system with dynamics endogenously linked at reintroduction. Using this methodology, there is evidence that lengthy reintroduction programs are not optimal. The solution to the black-footed ferret application indicates that translocation and reintroduction should either take place immediately or very early in the reintroduction program, or be delayed indefinitely, depending on economic values and the biology of the captive ferret population. The primary implication of this result is that, conditional on an acceptable level of uncertainty in the long-term persistence of the organism, species with viable habitat should be reintroduced immediately. We confirm this solution using brute-force numerical optimization.

## 2. Background

Black-footed ferrets are a type of mustelid native to the prairies and mountain grasslands of North America, famous for its 20th century decline and eventual status as extinct-in-the-wild. Its historical range comprised approximately 100 million acres (40.5 million hectares) of intermountain and prairie grasslands stretching from Canada to Mexico wherever prairie dogs occurred (Hillman and Clark, 1980; Anderson et al., 1986). Estimates of historic ferret populations range between half a million to one million individuals (Anderson et al., 1986).

However, starting at the end of the nineteenth century, the ferret population was gradually devastated by declines in prairie dogs due to habitat conversion, poisoning, and disease (USFWS, 2013). By 1964 ferrets were classified as “extremely rare” (Henderson et al., 1969), endangered in 1967 and 1970 (Udall, 1967; Russell, 1970), and presumed extinct in 1979 (USFWS, 2013). In 1981 a small population was discovered in Meeteetse, Wyoming (Clark, 1986). This population declined to 15 individuals (equivalent of 7 genetically-distinct founders) before it was placed in captivity to support a captive breeding and reintroduction program (USFWS, 2013). No wild populations have been found since the removal of the Meeteetse population - it is likely that all current black-footed ferrets are descended from those 15 individuals (Hanebury and Biggins, 2006).

Since 1991 there have been over 20 black-footed ferret reintroduction projects (USFWS, 2013; Tamkun and Gondrez, 2018). As of 2011, the U.S. Fish and Wildlife Service program had produced more than 7000 ferrets in captivity, of which more than 2600 had been translocated to the wild. Currently, population estimates suggest there are less than 500 breeding adult ferrets in the wild (USFWS, 2013). The scale of difference between the number of produced ferrets and the size of the existing wild population suggests there may be inefficiencies in the reintroduction program.

To delist black-footed ferrets as an endangered species, managers must establish several dozen black-footed ferret reintroduction sites with viable populations, which requires knowledge about the dynamics of ferrets and prairie dogs. Managers must be cognizant of the stock of prairie dogs prior to translocation as well as the potential ferret carrying capacity. If the number of ferrets exceeds what can be supported by the stock of prairie dogs, the prey will be overexploited and the ferret population will crash.

Implicitly, the delisting criteria must be satisfied without exceeding the funding allocated to the national reintroduction project. This means that managers are pursuing both ecological and economic goals. Costs are incurred in raising ferrets in captivity and managing prairie dogs in the wild (pre-introduction), and managing both prairie dogs and ferrets in the wild (post-introduction). As with other endangered species, there is an implicit assumption of infinite existence value. That is, the preservation of the species is paramount to any direct (harvest) or indirect (ecosystem service) benefits that the species might provide (Hartman, 1976; Brown and Shogren, 1998). Thus managers need to identify a reintroduction strategy that establishes viable populations in a least-cost manner.

## 3. Ecology

This section presents a basic, idealized population model of black-footed ferrets and prairie dogs. Black-footed ferrets are obligate predators, with prairie dogs comprising over 90% of their diet (Sheets et al., 1972; Campbell et al., 1987). Much is known about the demography of ferrets and prairie dogs (USFWS, 2013; Holmes, 2008; Miller et al., 1996; Hoogland et al., 1987; Knowles, 1982; Reading, 1993) though relatively little work has modeled these two species jointly as a predator-prey system (though see Bevers et al. (1997) and Klebanoff et al. (1991)).

Consider a potential black-footed ferret reintroduction site, e.g. a single patch that can support black-footed ferrets and prairie dogs. We

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