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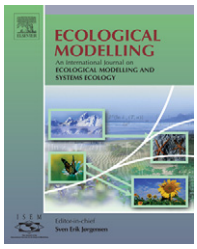

Optimal management of non-Markovian biological populations

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ABSTRACT

Wildlife populations typically are described by Markovian models, with population dynamics influenced at each point in time by current but not previous population levels. Considerable work has been done on identifying optimal management strategies under the Markovian assumption. In this paper we generalize this work to non-Markovian systems, for which population responses to management are influenced by lagged as well as current status and/or controls. We use the maximum principle of optimal control theory to derive conditions for the optimal management such a system, and illustrate the effects of lags on the structure of optimal habitat strategies for a predator–prey system.

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Substantial progress has been made in recent decades in the general area of informed natural resource management. Approaches to optimal decision making have been described and adopted in the management of various natural resources (reviewed by Williams, 1982, 1989; Williams et al., 2002). Such approaches include the ability to deal with sequential decisions for dynamical systems and even to incorporate in the optimization the reduction of uncertainty over time (e.g., Walters, 1986; Williams, 1996a,b; Williams and Nichols, 2001; Williams et al., 2002). Perhaps the most prominent use of these approaches in real world management involves the adaptive harvest management program for North American duck populations implemented in 1995 (Johnson et al., 1993, 1997; Nichols et al., 1995; Williams and Johnson, 1995; Williams et al., 1996).

Virtually all of the development for optimal decision processes in natural resources to date has involved the management of systems that can be characterized as first order Markov processes. For such processes, changes in system state between two times, t and $t+1$, depend only on system state at time t. However, for many biological systems it is difficult or impossible to adequately represent system dynamics without incorporating time lags. Hutchinson (1948) first considered the incorporation of a time lag in the Verhulst–Pearl logistic equation, such that the rate of change in population size at time t, dN/dt, is determined by population size at some previous time, $N_{(t-\tau)}$, where τ denotes the time lag. He noted that introduction of a lag induces oscillations, with system stability determined by the magnitude of the lag (Hutchinson, 1948). Leslie (1959) considered discrete time models in which age-specific survival and reproductive rates depended not only on abundance at the current time, but also on abundance at previous times. Leslie (1959) focused on the case in which abundance at the current time and at the time of birth of each age class (reflecting so-called cohort effects) were the relevant variables, and noted that lags of this form produced damped oscillations. In some species, probability of reproducing in year t is a function not only of conditions in year t, but also of whether or not the

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animal reproduced successfully the previous year (e.g., some sea turtles, Richardson et al., 1999; some albatross species, Weimerskirch et al., 1987; some whales, Fujiwara and Caswell, 2001). This biological lag can be modeled via the introduction of time lags or by definitions of state that incorporate past performance.

Wangersky and Cunningham (1957a,b) considered time lags in the response of predators to prey and in the responses of competitors to each other. Caswell (1972) reviewed previous analytic efforts to explore consequences of time lags and provided additional insights using simulation. May (1973) introduced time lags into models with two and three trophic levels, including vegetation–herbivore–carnivore systems.

In addition to the prevalence of time lags in models of system dynamics, the influences of management actions also may involve time lags. Various forms of habitat management, for example, are likely to be influenced by successional processes. These include forest management (e.g., Conroy and Moore, 2001) and use of fire as a management tool (e.g., Richards et al., 1999). In such instances, the state of populations of interest is influenced by the number of years elapsed, τ, since the last management action. There are multiple ways to model such time dependence, including the incorporation of time lags in animal population models and the simultaneous modeling of habitat state as a first order Markov process (e.g., Richards et al., 1999). Williams et al. (2002) discussed population dynamics of some familiar population models that incorporate lags in their transition equations.

Notwithstanding these efforts, there remains a need to be able to account more explicitly for previous biological states or previous management actions, especially as concerns managed biological systems. Our objective in this paper is to frame the issue of lagged effects in terms of optimal decision making, and to describe optimal strategies for lagged biological systems.

To that end, consider a biological population that is subjected to management over time, with time-specific actions based on current biological status and the projected effects of management on future status. For notational simplicity, biological status is characterized here by $x(t)$, representing elements such as cohort size, population status, or other indices of a natural resource system. Management action at time t is designated by $a(t)$, with policy $\{a(t)\}$ designating a sequence of actions over the time frame. Biological responses to actions typically are depicted by

$$x(t+1) = x(t) + f(x(t), a(t), t)$$

over the discrete time frame $\{t_0, t_0+1, \ldots, T\}$, and by

$$\dot{x} = f(x(t), a(t), t)$$

over the continuous time frame $[t_0, T]$. Not represented in these equations are environmental conditions and other factors that typically combine with biological status and management actions to influence biological change. The effects of these factors are implied by the argument t in the state transfer function.

A key feature of system dynamics as described above is that they are assumed to be Markovian, in that the change in system state depends on the current state but not on previous states. This assumption has important implications for both understanding and management of biological systems. In what follows we extend these models so as to accommodate non-Markovian state dynamics, according to

$$x(t+1) = x(t) + f(x(t), x(t-\tau), a(t), a(t-\tau), t)$$

and

$$\dot{x} = f(x(t), x(t-\tau), a(t), a(t-\tau), t).$$

In particular, we describe non-Markovian systems that include lags in the effects of system states, or management actions, or both.

1. Optimal control of Markovian populations

Irrespective of the occurrence of lags, benefits and costs attendant to management action can be captured in a function $U(a(t), x(t))$ describing the utility of action $a(t)$ when the population is of size $x(t)$. In discrete time the value associated with the control trajectory $\{a(t)\}$ is expressed in an objective functional

$$J = \sum_{t=t_0}^{T} U(a(t), x(t)) + F_1(x(T))$$

that includes accumulated utilities over the time frame and a terminal value function $F_1(x(T))$ that assigns value to the terminal system state $x(T)$. Thus, the optimal control problem for a Markovian system starting in state x_0 at time t_0 is

$$\underset{\{a(t)\}\in A}{\text{maximize}} \sum_{t=t_0}^{T} U(a(t), x(t)) + F_1(x(T))$$

subject to

$$x(t+1) = x(t) + f(x, a, t) \quad x(0) = x_0.$$

Here $\boldsymbol{A}$ represents admissible policies over $t \in \{t_0, t_0+1, \ldots, T\}$. In continuous time the problem is

$$\underset{\{a(t)\}\in A}{\text{maximize}} \int_{t_0}^{T} U(a(t), x(t))\mathrm{d}t + F_1(x(T))t$$

subject to

$$\dot{x} = f(x, a, t) \quad x(0) = x_0,$$

where the time index t can assume any value in the time frame $[t_0, T]$.

In words, we seek a control trajectory $\{a(t)\}$ that maximizes the objective functional, conditional on system dynamics and relevant system and control constraints. In this formulation, the transition equations act as equality constraints, along with the initial conditions and other operating conditions. For the remainder of this paper we focus on continuous-time problems, recognizing that an analogous argument can be fashioned for discrete-time systems. Unless needed for clarification, the time index for state variables and controls will be suppressed for notational convenience.

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