Integral control for population management

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Abstract

We present a novel management methodology for restocking a declining population. The strategy uses integral control, a concept ubiquitous in control theory which has not been applied to population dynamics. Integral control is based on dynamic feedback– using measurements of the population to inform management strategies and is robust to model uncertainty, an important consideration for ecological models. We demonstrate from first principles why such an approach to population management is suitable via theory and examples.

Keyowrds: integral control, PI control, population ecology, conservation, management

Mathematics Subject Classifcation (2010): 93C55, 93D15, 93C40, 92D25, 92D40

1 Introduction

Regulation or management to a constant set–point is fundamental across the natural and man–made world. Examples include the regulation of blood sugar by insulin (Saunders et al., 1998), bacterial chemotaxis in living cells (Yi et al., 2000), calcium homeostasis (El-Samad et al., 2002), the regulation of temperature in a central heating system (Haines and Hittle, 2003) or the navigation of a supertanker across stormy seas (Källström et al., 1979; Åström, 1980). Such examples span a huge range of time and length scales. In conservation management or pest control, population managers would aim to regulate the population to a desired density. A key feature in all of these applications is that set–point regulation must be robust to parametric uncertainty and observation errors. So how is such robust set–point regulation achieved? Yi et al. (2000) argue that the robustness of many homeostatic mechanisms must use integral control. Integral control is a simple yet powerful technique developed by control engineers, and is one component of a family of so–called PID – P for proportional, I for integral and D for derivative – controllers. PID controllers are used widely in industrial processes (Åström and Hägglund, 1995) and have been described as one of the "Success Stories in Control" (Samad and Annaswamy, 2011, p. 103). One striking feature of integral controllers, and PID controllers in general, is that they can be implemented on the basis of both minimal knowledge of the system to be managed or regulated, and in

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the presence of considerable system uncertainty. It is these two features that makes them appealing for population management/conservation.

Conservation is crucial to maintaining biodiversity and species viability in environments facing a range of pressures, such as those from habitat destruction, climate change, invasion and changing land use. Likewise, pest control or management is key to controlling unwanted or invasive populations which possibly have uncertain or unmodelled vital rates. However, that said, the first two sentences of the abstract of Walker (1998) read “Too much of wildlife management is today still more of an art than a science. Turning the art into a much needed predictive science requires including research in the management process.” In response to Walker’s claim there have been many theoretical approaches to population management in the ecological and conservation literature (see Section 2.1 for references). So far as we can tell, integral control (and PID control more generally) *has not* been considered as a technique for regulating a population by restocking or removing members. Here we present such an approach to conservation; describing how integral control arises naturally and is suitable for the task. In doing so we draw on a large body of existing theoretical work on integral control, which we adapt to a context of population management. Our focus in this manuscript is conservation and so we concentrate on supplementing populations. We comment, however, that managing a (possibly growing ambient) unwanted population to lower population densities can also be achieved using a *combined* proportional and integral (PI) control strategy.

The manuscript is organised as follows. Section 2 contains a nontechnical overview of integral control and describes the key concepts. Integral control, indeed PID control in general, is an extensively studied subject and it is clearly not possible, or indeed our purpose, to include a complete treatment here. Similarly, there are many other theoretical approaches to population management in the ecological and conservation literature, and in Section 2.1 we compare and contrast the methods proposed here to some existing techniques, such as partially observable Markov decision processes. Section 3 describes the mathematics of integral control and progressively adds additional features to the model necessitated by the specific demands of population modelling. These additional features are described on p. 8 and addressed sequentially in Sections 3.1–3.5. Throughout the manuscript we illustrate theoretical concepts with ecological examples. We seek to give a workable overview of integral control, the suitable modifications geared towards conservation using ecological models and cite relevant sources for further reading. We summarise our results and their potential applications in the discussion in Section 4.

2 Integral control for population conservation

Our objective is to present a method to restock a managed, but declining, population. We assume that the population is modelled by an age– or stage–structured (P)opulation (P)rojection (M)odel (Cushing, 1998; Caswell, 2001). These are discrete–time models where the time–steps are assumed fixed: a week, month, or breeding cycle for instance. First, we need to have access to an *observation* of the population. In a typical application, we do not know, and cannot measure, the entire population distribution at any given time; in fact, in practice there are stage–classes about which we have no knowledge. For instance, we might be able to measure population density of only the reproductive adults, and so in this case it is that stage only which is the observation. It is this part of the system which we seek to regulate. An important specification in the problem statement, therefore, is that only information of the measured stage–class (or classes) is available.

Second, we need to be able to replenish a stage (or combination of stages), that is, add new (or remove existing) population members. In a context of conservation, say of an endangered plant, such an action might be restocking by planting seedlings grown in a greenhouse. We describe a method for choosing management actions that result in the densities of the measured stages reaching a chosen reference value. Figure 2.1 contains a diagram of the setup described thus far.

The above problem fits naturally into a “classical” control theory setting, and we draw on techniques developed in that field to present a solution. A *precomputed* or *open–loop* control is a choice of manage-

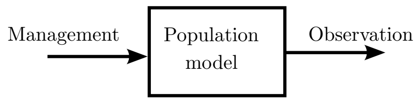
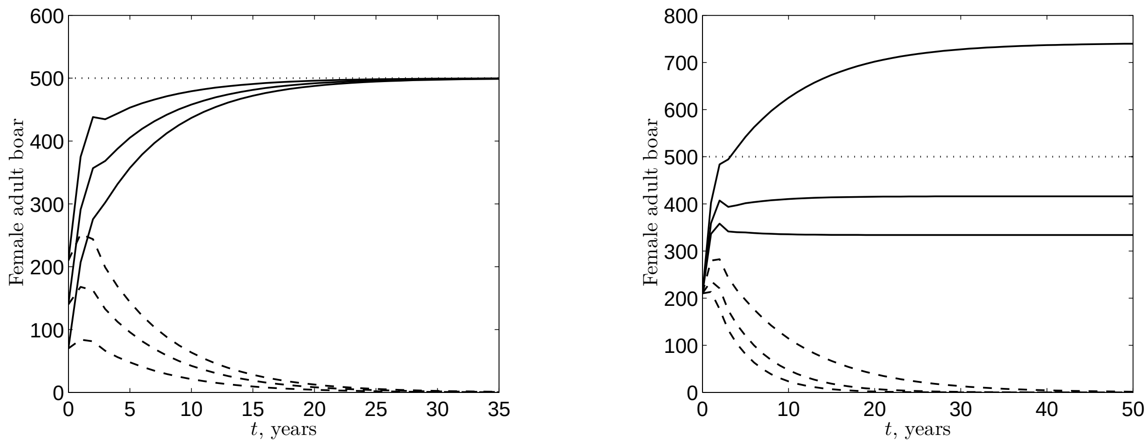


Figure 2.1: Diagram of the restocking scheme: management acts by adding or removing members of the population of certain stage–classes and a portion of the population is observed. The goal is to choose a management strategy so that the observed observations reach a chosen reference value.

ment strategy that is determined entirely by the model parameters and the chosen reference value. It is called open–loop because the corresponding block diagram, Figure 2.1, is an open loop – there is no feedback loop. It is straightforward to show that under mild assumptions on the model a suitably chosen constant management strategy, that is, a fixed number of new members of the population being added at each time–step results, in the observations converging to the reference value.

As an illustrative example, a matrix population projection model for females of the declining population of Wild Boar *Sus scrofa*, in poor environmental conditions, is given in Bieber and Ruf (2005). The matrix has three stage–classes, structured according to age. Suppose that at each time–step the density of the third stage–class, here denoting adult female boar, is measured. Similarly, assume that we have access to the same stage–class, so that we can release female adults into the population. The model is described in detail in Example 3.2 on p. 10. From each of three random initial population distributions our goal is to raise the female adult density to 500 (and to maintain that density). Here the chosen reference abundance is arbitrary but typical of wild boar density from Jedrzejewska et al. (1997, pp. 447–449). Figure 2.2 (a) contains the results of applying a precomputed control; the observed abundances of female adult boar of the unmanaged population are declining with time and the observed abundances of female adult boar of the managed population are converging to the target reference of 500.



(a) (b)

Figure 2.2: Precomputed control applied to the declining wild boar matrix PPM considered in Section 2. In both plots the solid lines and dashed lines denote observations with and without precomputed control respectively. The dotted lines denote the target reference abundance $r = 500$. (a) Observed female adult boar population. (b) Observed female adult boar with randomly perturbed model parameters.

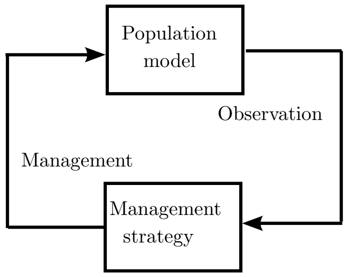
Precomputed control provides a simple method for raising population density via restocking. It does suffer from a major flaw, however. Precomputed control is not updated according to observations taken and requires exact knowledge of the model parameters in order to be implemented as intended. Ecological models are inherently noisy, often parameterised statistically from limited time–series data (Nichols et al., 1992), (Caswell, 2001, Chapter 6) and consequently there is wide scope for uncertainty. Uncertainty is a multi–faceted term in ecology (Williams, 2001; Regan et al., 2002) but here we specifically mean uncertainty in modelled vital rates. The upshot is that, when applying precomputed control to a (possibly highly) uncertain model, the management objective may not be achieved.

To demonstrate the sensitivity of precomputed control to model parameters, Figure 2.2 (b) contains projections of the wild boar projection model considered above, but with randomly perturbed model parameters. The precomputed control is based on the nominal estimate of these parameters; those given in Example 3.2. It is evident that the precomputed control does not achieve the desired outcome of 500 female adult boar in the presence of uncertainty. Although there are perturbations where the precomputed control does give rise to eventual observations *larger* than the reference r, there are also cases where the observations are *smaller* than r. Furthermore, in general it is *not* possible to predict the effect of arbitrary model uncertainty on the resulting observations of a precomputed control strategy, greatly limiting the appeal of precomputed control in this situation.

The problem statement, therefore, is: *design a method to restock a managed, but declining, population. The method should be implemented with only access to specified observations of that population and in a manner that is both independent of the initial population distribution and is robust to model uncertainty.*

Similar problem statements arise in many engineering contexts (as discussed earlier). It is well–known to engineers that the solution is to base the management strategy on a feedback law. In words, the management action to be taken at each time–step is based on observations of the population. Such a scheme is represented in Figure 2.3. Feedback control is often called *closed–loop* control because the loop in Figure 2.3 is closed.

Figure 2.3: Feedback control for population management: the management strategy is determined by the observations of that population. The goal is to design a management strategy so that the observed observations reach a chosen reference value.



Without yet going into the mathematical details; the choice of feedback control used depends on both the model to be controlled and the desired goal. The choice of feedback control is guided by the internal model principle (Francis and Wonham, 1976) which states that the controller, in this case the management strategy, must be able to reproduce the dynamics of the reference signal. Hence, if we wish to use a feedback control to regulate the population to a constant value, it will need to include an integrator and hence will be an integral controller. Furthermore, there is inherent robustness in this type of control, as we explain in Section 3.1.

In the remainder of the manuscript we demonstrate that integral control is a suitable feedback strategy for population management via restocking. We proceed in Section 3 to give a mathematical presentation of integral control. Figure 3.1 on p. 11 shows projections of the uncertain wild boar model subject to an integral control management strategy. We see that the desired outcome of 500 female adult boar is achieved.

Integral control, as presented in this manuscript, dates back to the 1970s and early contributions include Davison (1975, 1976), Lunze (1985), Morari (1985) and Grosdidier et al. (1985), while the later results we present draw on contemporary material derived by the present authors and their collaborators and which we cite in the text. We conclude this section with a brief overview of other modelling approaches to population management prevalent in the literature to which we compare and contrast integral control.

2.1 Comparison with existing approaches to population management

There are both deterministic and stochastic modelling approaches to population management in the literature. For populations modelled by matrix PPMs one approach is to investigate the effects of changing life history parameters on the dominant eigenvalue, which characterises the asymptotic growth rate of the population. A dominant eigenvalue greater than one gives rise to an asymptotically increasing population (under a few technical, but reasonable, mathematical conditions) and can be achieved by sufficient increase in the entries of the matrix specifying the PPM (Berman and Plemmons, 1994, p.27). A sensitivity (Demetrius, 1969) or elasticity (de Kroon et al., 1986) analysis can be used to quantify how small changes in particular vital rates affect the dominant eigenvalue; often guiding or even directing conservation efforts. Examples include, but are by no means restricted to, Crooks et al. (1998); Hunt (2001); Wilson (2003); Lubben et al. (2008) and Stott et al. (2012).

Biologically, the above procedure corresponds to improving the vital rates for a population, for example by improving the quality or access to food or by removing or limiting predation or poaching. Mathematically, the above procedure is a form of perturbation analysis and over recent years new tools have been added by Hodgson and Townley (2004); Hodgson et al. (2006); Deines et al. (2007); Lubben et al. (2009) to analytically describe the dependence of the dominant eigenvalue on the perturbation. These methods largely draw on the stability radius for robust control developed by Hinrichsen and Pritchard (1986a,b). The above framework is not directly comparable to integral control because (a) it is not a restocking or reintroduction scheme and (b) perturbations to vital rates are generally not modelled dynamically– they are considered as a static (that is, instant) intervention.

Stochastic models for population management are also prevalent in the literature. (M)arkov (D)ecision (P)rocesses (see, for example, Puterman (1994)) are, roughly speaking, Markov chains where at each time–step the state transition function depends on an action chosen by the modeller. Associated with each action and state are rewards (and/or costs), which are combined to form a so–called value function. As with feedback control, MDPs have been extended to the situation where, at each time–step, the entire state is not available to the modeller and instead only an observation (which is a stochastic or deterministic function of the state) is available. In this situation a (P)artially (O)bservable MDP is used instead. Since their inception POMDPs have been used in a wide variety of fields and we refer the reader to the surveys by Monahan (1982) or Dutech and Scherrer (2013) or the tutorial paper by Littman (2009) for examples and a history of their development. Worked examples in the conservation literature include Chadès et al. (2008, 2011) and POMDPs have also been applied for detecting and managing an ecological invasion, for example, in Haight and Polasky (2010) and Regan et al. (2011) and the references therein.

Although POMDPs are used in the literature with the same population management objective as that here (in some sense); we note that POMDPs are used in a slightly different fashion and consequently have different advantages and disadvantages. In the examples given above, the aim is to choose actions *optimally*, that is, to maximise the expected rewards obtained (and/or minimise the expected costs incurred) through the value function. Integral control is an example of feedback control– it is not an optimal control technique, and thus is a complimentary method. Two advantages of integral control are, first, that the models are very straightforward to use. This is especially pertinent because finding optimal policies for POMDPs is, in general, computationally very intensive (Cassandra, 1998), especially as the size of the state–space grows. The same is also true for models for population management that use (S)tochastic (D)ynamic (P)rogramming, such as Shea and Possingham (2000); McCarthy et al. (2001); Westphal et al. (2003); Tenhumberg et al. (2004) and Meir et al. (2004). Second, integral control is demonstrably robust to model uncertainty, a key consideration in ecological models. Optimal controls (including those obtained from classical results such as the Pontryagin Maximum Principle) are not always robust to model uncertainty (Doyle, 1978; Safonov and Fan, 1997); an increase in performance is traded–off against a loss of robustness. We are not aware of theoretical work on the robustness to model uncertainty or parameter uncertainty of the optimal solutions proposed by POMDPs in population management.

We conclude this section by remarking on active adaptive management (Walker, 1998; Shea et al., 2002; Williams, 2011). Precomputed control is an example of management that is not adaptive– the same number of individuals are released every time–step and no monitoring of the resulting population takes place. Conversely integral control, and feedback control more generally, is an example of active adaptive management. After every management event (that is, at each time–step) observations are collected and used to update the management action at the next step; this is the fundamental ingredient of feedback control, as depicted in Figure 2.3.

3 Mathematical formulation of integral control

This section contains a mathematical presentation of integral control for population management. We collect some notation; the symbols $\mathbb{R}^n$ and $\mathbb{C}^n$ denote real and complex n–dimensional Euclidean space respectively with $\mathbb{R}^1 = \mathbb{R}$ and $\mathbb{C}^1 = \mathbb{C}$ as standard. We let $\mathbb{R}^n_+$ denote the real nonnegative orthant and for vectors $a, b \in \mathbb{R}^n$, the inequality $a \geq b$ (equivalently $b \leq a$) is understood componentwise, so that $a \geq b$ means that $a - b \in \mathbb{R}^n_+$.

We first consider matrix PPMs (a treatment of some other classes of population models is addressed in Section 3.5). Suppose that the population can be described by n distinct age or stage–classes. If the population density in each stage–class is x_j, for $j = 1, \ldots, n$, then we let $x(t) = [x_1(t), x_2(t), \ldots, x_n(t)]^T$ denote the population vector which has dynamics described by the matrix PPM

$$x(t+1) = Ax(t), \quad x(0) = x^0, \quad t = 0, 1, 2, \ldots, \tag{3.1}$$

where x^0 denotes the initial population distribution. Throughout this manuscript we assume that the (unmanaged) population modelled by (3.1) is in asymptotic decline for every initial population distribution x^0, which means that the *spectral radius* of A is less than one. Recall that the spectral radius of a matrix M, denoted $\rho(M)$, is defined as

$$\rho(M) = \lim_{t \to \infty} \|M^t\|^{\frac{1}{t}}, \tag{3.2}$$

(where $\|\cdot\|$ denotes any matrix norm) which captures the asymptotic growth rate of the norm of M^t. Since we shall always consider matrices A that are componentwise nonnegative it follows from, for instance Berman and Plemmons (1994, p.26), that the spectral radius of A equals the dominant eigenvalue (which for such matrices is accordingly also named the *asymptotic growth rate*). In order to state our results concisely we record our key assumptions. Based on the above discussion, the first assumption is

(A1) the real $n \times n$ matrix A is componentwise nonnegative with $\rho(A) < 1$.

Recall the enforced assumption that we (probably) do not know the entire population distribution $x(t)$ in (3.1) precisely because there are stage–classes about which we have no information. It is quite probable, for instance, that the full initial population distribution x^0 is unavailable. However, we assume that we do have access to a measured variable, or observation, $y(t)$ described by

$$y(t) = c^T x(t), \quad t = 0, 1, 2, \ldots. \tag{3.3}$$

The variable $y(t)$ represents the total knowledge about $x(t)$ available for management decisions, and might take the form of the results of a census or survey. Here c in (3.3) is a column vector so that c^T is a row vector, called the observation vector. We let the superscript ^{T} denote matrix transposition. By way of an example, suppose that we are considering a population with five stage–classes. If the abundance of the penultimate stage is measured at each time–step, then

$$c^T = \begin{bmatrix} 0 & 0 & 0 & 1 & 0 \end{bmatrix}, \quad \text{with} \quad y(t) = c^T x(t) = x_4(t).$$

The second facet of the model is to allow the population to be supplemented or depleted by the arrival or removal of new members respectively. To describe this we include a control term $bu(t)$ in (3.1), to obtain the controlled population model

$$x(t+1) = Ax(t) + bu(t), \quad x(0) = x^0, \quad t = 0, 1, 2, \ldots. \tag{3.4}$$

The term $bu(t)$ describes the addition ($bu(t) \geq 0$) or removal ($bu(t) < 0$) of population members distributed across population stages through the column vector b. The vector b is the choice of the modeller, although probably subject to implementation constraints. The population model (3.4) together with the observation (3.3) is combined to give

$$\left.\begin{aligned} x(t+1) &= Ax(t) + bu(t), \quad x(0) = x^0, \\ y(t) &= c^T x(t), \end{aligned}\right\} \quad t = 0, 1, 2, \ldots. \tag{3.5}$$

In the context of Section 2, the time–dependent variable $u(t)$ in (3.5) is the management strategy and $y(t)$ in (3.5) is the observation, both at time–step t.

Recalling that we do not know the population $x(t)$ exactly, we are interested in what effect $u(t)$ has on $y(t)$. Under assumption **(A1)**, the linearity of (3.5) means that it is straightforward to demonstrate that if

$$\lim_{t\to\infty} u(t) = \tilde{u}\,, \quad \text{then} \quad \lim_{t\to\infty} y(t) =: \tilde{y} = c^T(I-A)^{-1}b\tilde{u}\,, \tag{3.6}$$

where I denotes the $n \times n$ identity matrix. The constant $c^T(I-A)^{-1}b$ in (3.6) is called the *steady state gain* as it is the multiplier (the gain) that when applied to a constant input signal gives the resulting eventual observation. Using the fact that

$$c^T(I-A)^{-1}b = \sum_{k=0}^{\infty} c^T A^k b = c^T(I + A + A^2 + \ldots)b\,, \tag{3.7}$$

another interpretation of the steady–state gain is that it is the measured cumulative contribution to the observation over all time from a constant influx of $\tilde{u} = 1$ population members structured by b. When b and c are nonnegative vectors then from (3.7) it follows that $c^T(I-A)^{-1}b \geq 0$ as well. If $c^T(I-A)^{-1}b > 1$ then $\tilde{u}$ is amplified after a long period of time and conversely if $c^T(I-A)^{-1}b < 1$ then $\tilde{u}$ it is attenuated.

Assuming that $c^T(I-A)^{-1}b > 0$, we see from (3.6) that in order for the observations to eventually reach a chosen value r, so that $\tilde{y} = r$, then

$$u(t) = \tilde{u} := \frac{r}{c^T(I-A)^{-1}b}, \quad t = 0, 1, 2, \ldots\,, \tag{3.8}$$

and this precomputed control achieves $y(t)$ tending to r for any initial population distribution x^0. Our second assumption rules out the (degenerate) case that the steady–state gain of A, b, c^T is zero

(A2) the matrix A and vectors b and c^T are such that $c^T(I-A)^{-1}b > 0$.

We remark that **(A2)** is always satisfied if A satisfies **(A1)**, A is irreducible and b and c^T are nonnegative and nonzero. Irreducibility is a natural assumption for ecologically meaningful PPMs (Stott et al., 2010) and hence assumption **(A2)** is not overly restrictive.

The integral control feedback scheme is the dynamic, time–dependent strategy

$$u(0) = u^0, \quad u(t) = u^0 + g\sum_{j=0}^{t-1}(r - y(j)), \quad t = 1, 2, \ldots\,, \tag{3.9}$$

where r is the chosen reference value, $g > 0$ is a design parameter (often called the "gain" parameter) and the value of u^0 is arbitrary. The strategy (3.9) is a "discrete time integrator" because at time–step t the control signal $u(t)$ is determined by summing (equivalently "integrating in discrete time") the previous deviations of the observation $y(t)$ from the reference r. The combination of (3.5) and (3.9) leads to the feedback system

$$\left.\begin{aligned} x(t+1) &= Ax(t) + bu(t)\,, & x(0) &= x^0\,, \\ u(t+1) &= u(t) + g(r - c^T x(t))\,, & u(0) &= u^0\,, \end{aligned}\right\} \quad t = 0, 1, 2, \ldots\,. \tag{3.10}$$

Before stating the first result we need some more notation. The transfer function G of the linear system (3.5) is defined by

$$z \mapsto G(z) := c^T(zI - A)^{-1}b\,, \quad z \in \mathbb{C}\,, \tag{3.11}$$

which is certainly defined for every complex z that is not an eigenvalue of A. The transfer function is a ubiquitous concept in control engineering with many uses, and has also been used in ecological modelling (Hodgson and Townley, 2004). For our present purposes it is sufficient to note that under assumption **(A1)** the steady–state gain is equal to $G(1)$, the transfer function evaluated at one.

Theorem 3.1. *Assume that the linear system* (3.5) *satisfies assumptions* **(A1)** *and* **(A2)**. *Then there exists* $g^* > 0$ *such that for all* $g \in (0, g^*)$, *every* $r > 0$ *and all initial conditions* $(x^0, u^0) \in \mathbb{R}_+^n \times \mathbb{R}_+$, *the solution* (x, u) *of* (3.10) *has the following properties:*

(1) $\lim_{t\to\infty} u(t) = \dfrac{r}{G(1)}$,

(2) $\lim_{t\to\infty} x(t) = (I - A)^{-1} b \dfrac{r}{G(1)}$,

(3) $\lim_{t\to\infty} y(t) = \lim_{t\to\infty} c^T x(t) = r$.

We refer the reader to Logemann and Townley (1997) for a proof of the above result. However, we provide here an illustration of both how integral control works and the role of the gain parameter g. First, note that if (x^*, u^*) is an equilibrium of the feedback system (3.10), then by definition

$$\begin{aligned} x^* &= Ax^* + bu^* & &\Rightarrow & x^* &= (I - A)^{-1} b u^*\,, \\ u^* &= u^* + g(r - c^T x^*) & &\Rightarrow & c^T x^* &= r\,, \end{aligned} \tag{3.12}$$

where for the second implication we have used that $g > 0$. The final equality in (3.12) shows that the x^* component of *any* equilibrium (x^*, u^*) of (3.10) gives rise to an output $c^T x^*$ equal to the reference r. Theorem 3.1 is proven, therefore, as soon as the existence of a global asymptotically stable equilibrium of (3.10) is established. To that end a short calculation using (3.12) shows that the feedback system (3.10) can be written as

$$\begin{bmatrix} x(t+1) - x^* \\ u(t+1) - u^* \end{bmatrix} = \underbrace{\begin{bmatrix} A & b \\ -gc^T & 1 \end{bmatrix}}_{=:A_g} \begin{bmatrix} x(t) - x^* \\ u(t) - u^* \end{bmatrix}, \quad t = 0, 1, 2, \ldots . \tag{3.13}$$

By inspection of (3.13) we see that Theorem 3.1 holds precisely for $g > 0$ such that $\rho(A_g) < 1$, where recall that $\rho(A_g)$ is the spectral radius of A_g. Under assumption **(A1)**, when $g = 0$ the eigenvalues of A_0 are those of A and one and thus $\rho(A_0) = 1$. However, for small but positive g it can be shown that $\rho(A_g) < 1$. If g is too large then $\rho(A_g) \geq 1$ and the theorem fails. As such, Theorem 3.1 is a so–called "low–gain" result since it guarantees that, if the gain parameter g is small enough, then the control objective is achieved. Consequently, in these circumstances integral control provides a solution to our original problem of restoring population levels via restocking, in a manner that only requires knowledge of the available observations $y(t)$ and for any initial population distribution x^0.

The conclusions (1)–(3) of Theorem 3.1 demonstrate that the integral controller (3.10) solves the replenishment problem. The model (3.10) is reasonably general and is suited to a wide range of scientific and engineering applications. In the context of population management, the following potential problems need to be addressed:

(P1) *What types of uncertainty can integral control tolerate?* Ecological systems are inherently noisy, with many forms of uncertainty that the model (3.10) does not yet address.

(P2) *Can integral control be extended to incorporate additional feasibility constraints on the input* $u(t)$*?* The feedback strategy (3.9) can generate either very large or negative values of $u(t)$. Large input signals might be too large for practical implementation given limited resources. Negative $u(t)$ requires managers to remove members from the population, which seems illogical when our ultimate goal is to boost or at least conserve population density. Negative control signals may even result in the integral control system (3.10) predicting negative populations, which is clearly absurd.

(P3) *How small does the gain* g *in the feedback strategy* (3.9) *need to be?* Theorem 3.1 requires that the parameter g is small enough and although it is always possible to choose such a g, the theorem gives no indication of what this is or how to find it.

(P4) *Can the rate of convergence of the observations to the reference be improved?* Theorem 3.1 guarantees that the observations converge to the reference, but the integral control model (3.10) does not yet include additional features that can alter the rate of convergence.

(P5) *Can integral control be applied to other population models?* Matrix PPMs model a single population in discrete stage–classes and, for example, have no explicit spatial component.

Sections 3.1–3.5 sequentially address the above problems. Each subsection begins with a verbal outline of the solution that proceeds the mathematical details. Section 3.6 describes how the solutions of these problems combine.

3.1 *What types of uncertainty can integral control tolerate?*

Here we describe types of uncertainty likely to be present in integral control and qualify the extent to which integral control can tolerate these uncertainties **(P1)**.

Several authors have proposed frameworks for describing (and indeed reducing) uncertainty in ecological modelling, and we shall appeal to the terminology of Williams (2001) (see also Williams (2011, Section 4)) and Regan et al. (2002). Since we are describing the modelling aspects of integral control, we are focussing on *epistemic uncertainty*, in the language of Regan et al. (2002), as opposed to *linguistic uncertainty*. Mathematically, we argue that there are three types of uncertainty present that integral control needs to be able cope with: *(i)* model uncertainty, *(ii)* measurement errors, *(iii)* activation errors. The connections between these descriptions and those already established in the literature are described in Table 1 below.

Table 1: Connecting types of uncertainty to which integral control is subject with existing descriptions of uncertainty in the ecology literature.

	Williams (2001)	Regan et al. (2002)
(i)	Environmental variation Structural uncertainty	Natural variation Inherent randomness Model uncertainty
(ii)	Partial observability	Measurement error Systematic error
(iii)	Partial controllability	

Robust control is an important and well–studied topic in control engineering with many textbooks dedicated to the subject (for example, Doyle et al. (1992); Green and Limebeer (1995); Zhou et al. (1996) and Zhou and Doyle (1998)). Quoting Doyle et al. (1992, p. 8), "Generally speaking, the notion of robustness means that some characteristic of the feedback system holds for every plant in the set P." The term *plant* in control engineering denotes the model to be studied or controlled and comes historically from power or chemical plants. We need to identify the *set of plants* and the desired *characteristics*. In our context the set of plants P is all integral control models of the form (3.10) with the collection of uncertainties *(i)*–*(iii)*. The desired characteristics to hold are the conclusions of Theorem 3.1. Quoting Green and Limebeer (1995, p. xi), "Systems that can tolerate plant variability and uncertainty are called robust–. . . " We now discuss the types of uncertainty in detail.

(i): Model uncertainty amounts to not knowing the model parameters A, b and c^T in (3.1). Uncertainty in A can arise quite naturally. Parameter values in A may be only estimates or statistical means of some "true" value. Or, the structure of A may be uncertain. For instance, A could be age–structured or stage–structured, which can model the same underlying process but have different mathematical realisations. In some cases the input vector b will be known, for example, when b represents restocking into a well–defined developmental stage–class in the model. However, b could be uncertain; say, when restocking seedlings which recruit into an unknown distribution of size classes. Often the observation vector c^T is known, for the same reason as b– when c^T captures counting abundance of a well–defined development stage, such as female nesting adult turtles. However, c^T could be uncertain; in a size based model, not all of the stage–classes need to be specified in order to count the abundances of a given size. Such a

situation leaves c^T unknown. Finally, the dimension n of the model itself could be uncertain. Integral control is robust to all of these model uncertainties for the following reasons.

The two crucial assumptions placed on the model parameters A, b and c^T for integral control are **(A1)** and **(A2)**. Assumption **(A1)** does not require knowledge of A and holds for any population model of the form (3.1) in asymptotic decline. Similarly, assumption **(A2)** does not require knowledge of A, b and c^T, or indeed the exact value of $G(1) = c^T(I - A)^{-1}b$, only that it is positive, which is true when A is nonnegative and irreducible and b and c^T are nonnegative and nonzero. As we have commented earlier, irreducibility is a natural assumption for matrix PPMs (Stott et al., 2010). Knowledge of A, b or c^T is not needed for the implementation of integral control. In fact, assumptions **(A1)** and **(A2)** are necessary for low–gain integral control and so we cannot allow greater uncertainty.

Example 3.2. The wild boar matrix PPM considered in Section 2 has matrix A, control vector b and observation vector c^T given by

$$A = \begin{bmatrix} 0.13 & 0.56 & 1.64 \\ 0.25 & 0 & 0 \\ 0 & 0.31 & 0.58 \end{bmatrix}, \quad b = \begin{bmatrix} 0 \\ 0 \\ 1 \end{bmatrix}, \quad c^T = \begin{bmatrix} 0 & 0 & 1 \end{bmatrix}. \tag{3.14}$$

For the simulations in Figure 3.1 each of the non–zero entries of A is randomly perturbed by up to 20%. The same gain parameter of $g = 0.12$ is used for each simulation. We see that each simulated observation converges to the reference $r = 500$. However, the total female population densities and the number of new individuals added per time–step in Figures 3.1 (b) and 3.1 (c) respectively are converging to different limits. This is because by Theorem 3.1 (1) and (2), the respective limits

$$\lim_{t\to\infty} \|x(t)\|_1 = \lim(x_1(t) + x_2(t) + x_3(t)) = \left\|(I - A)^{-1}b\frac{r}{G(1)}\right\|_1 \quad \text{and} \quad \lim_{t\to\infty} u(t) = \frac{r}{G(1)},$$

both depend on A (noting that $G(1)$ also depends on A), which is being perturbed in this example.

(ii): Observation errors. The integral control model (3.10) assumes that the observations $y(t)$ taken at each time–step are correct. In practice there are bound to be errors incurred in the counting or measuring process. This is conceivably a problem because the integrator (3.9) feeds back the observation $y(t)$ into the control signal.

Here we describe how integral control responds in the presence of measurement errors. In what follows $y(t)$ denotes the *measured* observation, whilst the *actual* observation is $c^T x(t)$. As always we are assuming that A, b and c^T in (3.5) satisfy **(A1)** and **(A2)** and further that $g > 0$ in (3.9) is chosen sufficiently small so that Theorem 3.1 holds for the integral control system (3.10). A general additive observation error $d(t)$ can be incorporated into (3.10) as

$$\left.\begin{aligned} x(t+1) &= Ax(t) + bu(t), \qquad x(0) = x^0, \\ y(t) &= c^T x(t) + d(t), \\ u(t+1) &= u(t) + g(r - y(t)), \quad u(0) = u^0, \end{aligned}\right\} \quad t = 0, 1, 2, \dots. \tag{3.15}$$

If $d(t)$ equals a constant $\tilde{d}$ for each t (that is, a constant systematic observation error is made), or $d(t)$ converges to $\tilde{d}$, then it is elementary to demonstrate that the measured variable $y(t)$ converges to $r - \tilde{d}$. In words, there is offset in the tracking.

If $d(t)$ is periodic (the observation error is seasonal for example), say $d(t) = \tilde{d}\cos(\theta t)$ for some $\tilde{d} \in \mathbb{R}$ and $\theta > 0$, then again it is elementary to demonstrate that the measured variable $y(t)$ settles to the periodic signal

$$r - \tilde{d}A_\theta \cos(\theta t + \phi_\theta),$$

which oscillates around r with magnitude $\tilde{d}A_\theta$ and phase shift ϕ_θ, where

$$A_\theta = \left|\frac{gG(e^{i\theta})}{e^{i\theta} - 1}\left(1 + \frac{gG(e^{i\theta})}{e^{i\theta} - 1}\right)^{-1}\right| \quad \text{and} \quad \phi_\theta = \arg\left(\frac{gG(e^{i\theta})}{e^{i\theta} - 1}\left(1 + \frac{gG(e^{i\theta})}{e^{i\theta} - 1}\right)^{-1}\right).$$

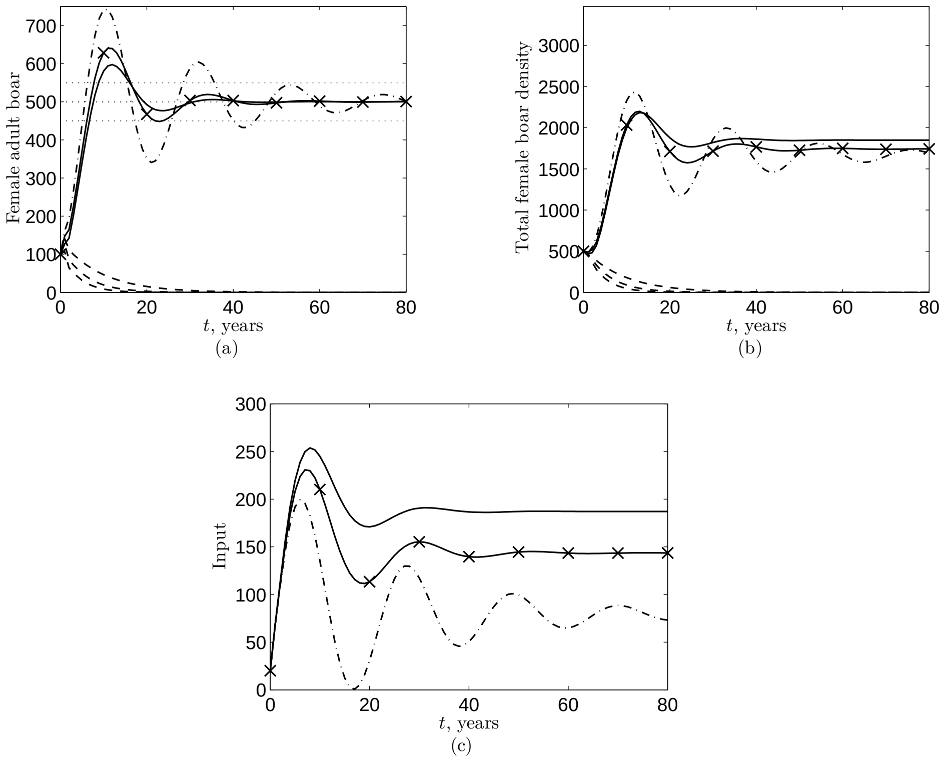


Figure 3.1: Integral control (3.10) applied to the declining wild boar matrix PPM of Example 3.2 with randomly perturbed model parameters. In each plot the solid, solid–crossed and dashed–dotted lines are corresponding simulations subject to the integral control system (3.10). The dashed lines are projections from the uncontrolled model (3.1). (a) Observations of female adult boar. The dotted lines are the reference $r = 500$ and $r \pm 10\%$. (b) Total female population density. (c) The number of new individuals added at each time–step, determined by the integral control management strategy (3.9).

For complex z, the notation $\arg(z)$ denotes the argument of z. For arbitrary additive observation error $d(t)$ one can show that

$$\limsup_{t\to\infty} |y(t) - r| \le \mu_g \limsup_{t\to\infty} |d(t)|, \tag{3.16}$$

where the constant μ_g can be computed and is given in Appendix A.1. The significance of the bound in (3.16) is that for large t the error between the measured observation and the reference is linear in the magnitude of $d(t)$.

It is important to note that assumptions **(A1)** and **(A2)** and the size of the gain parameter g are all independent of measurement errors when these errors occur additively, as in (3.15).

Example 3.3. Simulations of the integral control system with additive output error (3.15) applied to the wild boar model of Example 3.2 are plotted in Figure 3.2. For the same A, b, c^T, x^0, u^0, r and g as in that example, Figure 3.2 (a) contains three projected observations subject to the additive observation errors plotted in Figure 3.2 (b). The specific $d(t)$ considered are constant with value -50 (solid), convergent to 125 (dashed) and periodic (dashed–dotted). The resulting observations are convergent to $r - d = 500 - (-50) = 550$, $500 - 125 = 375$ and periodic respectively.

A potentially more plausible description of observation error is that it is proportional to the observation taken, which we describe by

$$y(t) = (1 + \varepsilon(t))c^T x(t), \quad t = 0, 1, 2, \ldots. \tag{3.17}$$

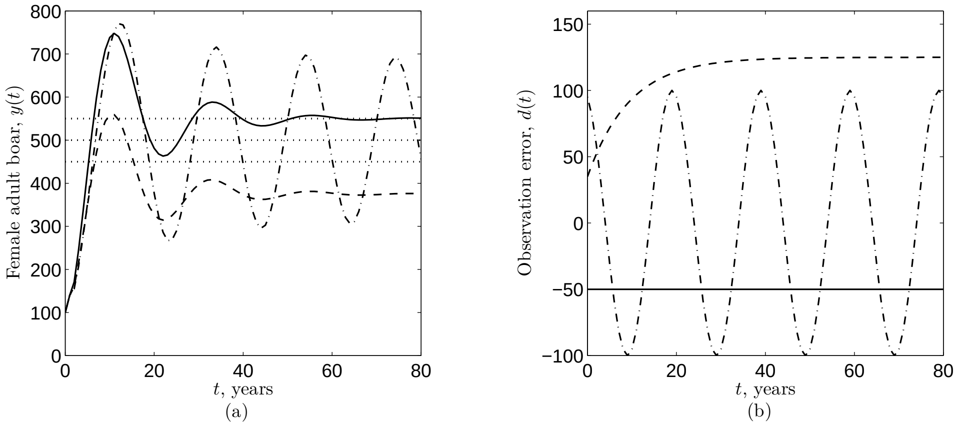


Figure 3.2: Integral control with additive observation errors (3.15) applied to the wild boar matrix PPM of Example 3.2. See Example 3.3. (a) Observations. The dotted lines are the reference $r = 500$ and $r \pm 10\%$. (b) Observation errors.

The term $\varepsilon(t)$ is the error which is unknown and assumed to be close to zero. For example, $\varepsilon(t)$ taking the values -0.1, -0.12 and 0.05 in three consecutive time–steps corresponds to measuring 90%, 88% and then 105% of the actual population respectively. The case $\varepsilon(t) = 0$ corresponds to the measured and actual observations coinciding so that (3.3) is recovered. We assume that $\varepsilon(t) > -1$ for every t, so that a positive observation is always taken. For applications, what is often important is knowing the "worst case scenario", which amounts to knowing the largest possible observation errors.

If we assume that the observation errors are random, that is, each $\varepsilon(t)$ is a random variable, then each observation $y(t)$ is also a random variable. The main result of this section is Theorem 3.4 below which states that if the errors are assumed (I)ndependent and (I)dentically (D)istributed then the expectation of the observations $y(t)$ converge to the reference r. If additionally the variance of the errors is not too large then the variance of the observation $y(t)$ converges to a finite computable quantity.

Let $\otimes$ denote the Kronecker product and $0_{m\times p}$ denote the $m \times p$ zero matrix.

Theorem 3.4. *Assume that the linear system* (3.5) *satisfies assumptions* **(A1)** *and* **(A2)** *and that* $g > 0$ *is such that*

$$\rho(A_g) < 1, \quad \text{where} \quad A_g = \begin{bmatrix} A & b \\ -gc^T & 1 \end{bmatrix}.$$

Assume that $(\varepsilon(t))_{t=0}^{\infty}$ *is a sequence of IID random variables with zero mean and variance* σ^2 *and let* $y(t)$ *denote the measured observations of the integral control system* (3.10) *with observation error* (3.17). *It follows that*

(1) $y(t)$ *converges in expectation to* r, *that is,* $\lim_{t\to\infty} \mathbb{E}(y(t)) = r$.

(2) *If*

$$\sigma^2 < \frac{1}{g^2 \max\limits_{|z|=1} |\tilde{E}(zI - A_g \otimes A_g)^{-1}\tilde{D}|}, \quad \text{where} \quad \begin{aligned} \tilde{D} &= \begin{bmatrix} 0_{1\times(n^2+2n)} & 1 \end{bmatrix}^T, \\ \tilde{E} &= \begin{bmatrix} (c^T \quad 0) \otimes (c^T \quad 0) \end{bmatrix}, \end{aligned} \tag{3.18}$$

then

$$\lim_{t\to\infty} \operatorname{var} y(t) = \begin{bmatrix} c^T & 0 \end{bmatrix} C_\infty \begin{bmatrix} c \\ 0 \end{bmatrix} < \infty.$$

Here the matrix $C_\infty = C_\infty^T$ *solves the symmetric linear matrix equation (Ran and Reurings, 2002)*

$$C_\infty - A_g C_\infty A_g^T - g^2\sigma^2(DE)C_\infty(DE)^T - g^2 r^2 \sigma^2 DD^T = 0,$$

where

$$D = \begin{bmatrix} 0_{1\times n} & 1 \end{bmatrix}^T, \quad \text{and} \quad E = \begin{bmatrix} c^T & 0 \end{bmatrix}.$$

A proof of the above theorem is given in Appendix A.2, where an algorithm is also provided for finding C_∞. The quantity on the right hand side of (3.18) can be readily computed numerically, and provides an estimate for the largest permitted variance in observation error so that the resulting observation has finite variance.

Example 3.5. Theorem 3.4 is applied to the wild boar model of Example 3.2. For the same A, b, c^T, x^0, u^0, r and g as in that example the integral control system (3.10) with proportional observation error $\varepsilon(t)$ as in (3.17) is simulated. The errors $\varepsilon(t)$ are normally distributed with zero mean and constant variance $\sigma^2 = 0.09$. Figure 3.3 (a) plots three observation simulations $y(t)$ as well as the expected observation $\mathbb{E}(y(t))$. Figure 3.3 (b) contains the corresponding three sequences of input signals $u(t)$, as well as the expected input sequence. In this example the variance of $y(t)$ converges to $\sim 7,600$, so that the standard deviation of $y(t)$ is ~ 87, and the constant in (3.18) equals 3.04. Hence, in this example the variance of $y(t)$ will converge for any observation error with $\sigma^2 < 3.04$.

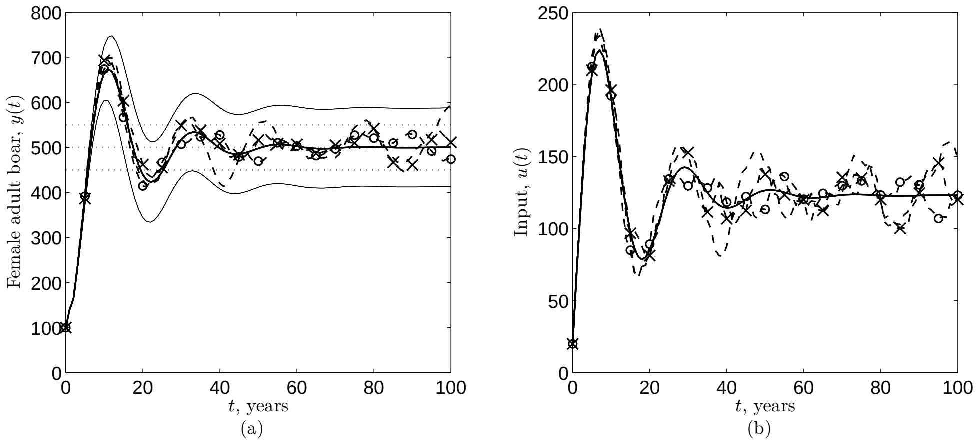


Figure 3.3: Integral control with proportional observation errors (3.10), (3.17) applied to the wild boar matrix PPM of Example 3.2. See Example 3.5. (a) Observations plotted in dashed, dashed–circled and dashed–crossed lines. The solid lines are the expected observation $\mathbb{E}(y(t))$ and $\mathbb{E}(y(t)) \pm \sqrt{\operatorname{var} y(t)}$. The dotted lines are the reference $r = 500$ and $r \pm 10\%$. (b) Inputs plotted in the matching line style as the corresponding observations in (a).

(iii): Activation errors. The integral control model (3.10) assumes that the input signals are exact, that is, the number of individuals specified by the integral control strategy (3.9) is equal to the number of individuals released (or planted and so on) at each time–step. In the context of restocking schemes we expect that activation errors are (generally) less prevalent than measurement errors, and so only give a brief treatment. Accommodating an additive activation error $d(t)$, (3.10) becomes

$$\left.\begin{aligned} x(t+1) &= Ax(t) + b(u(t) + d(t)), \quad && x(0) = x^0, \\ y(t) &= c^T x(t), && \\ u(t+1) &= u(t) + g(r - y(t)), && u(0) = u^0, \end{aligned}\right\} \quad t = 0, 1, 2, \ldots, \tag{3.19}$$

where g is small enough so that the conclusions of Theorem 3.1 apply to the integral control system (3.10). One advantage of integral control is it *rejects* constant, or convergent activation errors. Specifically, if $d(t)$ equals a constant $\tilde{d}$ for each t (that is, a constant systematic activation error is made), or $d(t)$ converges to $\tilde{d}$, then the observations $y(t)$ still converge to r.

The effects of periodic or general additive activation errors on the observations mirror those in the observation errors case. Specifically, if $d(t) = \hat{d}\cos(\omega t)$ for some $\hat{d} \in \mathbb{R}$ and $\omega > 0$, then again it is elementary to demonstrate that the measured variable $y(t)$ settles to the periodic signal

$$r + \hat{d} M_\omega \cos(\omega t + \psi_\omega),$$

which oscillates around r with magnitude $\hat{d}M_\omega$ and phase shift ψ_ω, where

$$M_\omega = \left|\frac{(\mathrm{e}^{\mathrm{i}\omega}-1)G(\mathrm{e}^{\mathrm{i}\omega})}{\mathrm{e}^{\mathrm{i}\omega}-1+gG(\mathrm{e}^{\mathrm{i}\omega})}\right| \quad \text{and} \quad \psi_\omega = \arg\left(\frac{(\mathrm{e}^{\mathrm{i}\omega}-1)G(\mathrm{e}^{\mathrm{i}\omega})}{\mathrm{e}^{\mathrm{i}\omega}-1+gG(\mathrm{e}^{\mathrm{i}\omega})}\right).$$

For arbitrary additive activation errors $d(t)$ one can show that

$$\limsup_{t\to\infty} |y(t)-r| \le \nu_g \limsup_{t\to\infty} |d(t)|, \tag{3.20}$$

where the constant ν_g is given in Appendix A.1. As with the estimate (3.16), the bound (3.20) depends linearly on the magnitude of the activation error. As with observation errors, we note that assumptions **(A1)** and **(A2)** and the size of the gain parameter g are all independent of the activation errors considered in (3.19).

3.2 *Can integral control be extended to incorporate additional feasibility constraints on the input $u(t)$?*

If we require that the input $u(t)$ satisfies $0 \le u(t) \le U$, where U is a chosen per time–step upper bound, and if the reference r is such that $0 < r < G(1)U$ then a (modified) integral control model still achieves the desired control objective **(P2)**. Furthermore, if $r \ge G(1)U$ then the control objective *cannot* be solved by replenishment alone. The main result of this section which establishes the above claims is Theorem 3.6, and is a special case of Coughlan and Logemann (2009, Theorem 3.2).

We bound the input in the integral control system (3.10) by applying a filter to the input. To that end we introduce the saturation nonlinearity ϕ, which replaces negative control signals by zero and includes the upper bound U chosen by the modeller for the maximum control signal:

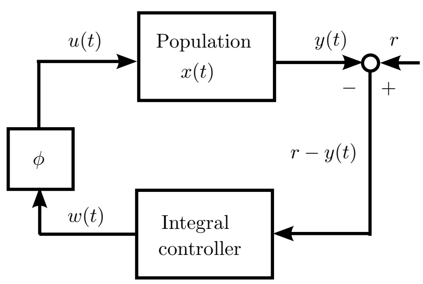
$$\phi:\mathbb{R}\to\mathbb{R}, \quad \phi(v) := \begin{cases} 0, & v<0 \\ v, & 0 \le v \le U \\ U, & U < v \end{cases}. \tag{3.21}$$

The feedback system (3.10) is replaced by

$$\left.\begin{aligned} x(t+1) &= Ax(t)+bu(t), & x(0)&=x^0,\\ w(t+1) &= w(t)+g(r-c^Tx(t)), & w(0)&=w^0,\\ u(t) &= \phi(w(t)), \end{aligned}\right\} \quad t=0,1,2,\ldots. \tag{3.22}$$

The inclusion of ϕ in (3.22) ensures that a nonnegative population is always predicted. The scalar $w(t)$ is the integrator state, and is generated by the integrator (3.9). The control $u(t)$ is the *filtered* integrator state $\phi(w(t))$. Figure 3.4 contains a diagram of this arrangement.

Figure 3.4: Block diagram of the feedback system (3.22). The control signal $u(t)$ applied to the population equals the filtered integrator state $\phi(w(t))$, where $w(t)$ is generated by the integrator (3.9).



In addition to tackling **(P2)**, Theorem 3.6 also provides the upper bound $1/|\gamma|$ for the integrator gain g, where the constant γ is given by

$$\gamma := \sup_{q\ge 0}\left\{\inf_{\theta\in[0,2\pi)} \mathrm{Re}\left[\left(\frac{q}{\mathrm{e}^{i\theta}}+\frac{1}{\mathrm{e}^{i\theta}-1}\right)G(\mathrm{e}^{i\theta})\right]\right\} \in \mathbb{R}, \tag{3.23}$$

and G is the transfer function from (3.11).

Theorem 3.6. *Assume that the linear system* (3.5) *satisfies assumptions* **(A1)** *and* **(A2)** *and let* γ *be as in* (3.23)*. Then, for every* $U > 0$*, every* $r \in (0, G(1)U)$*, every* $g \in (0, 1/|\gamma|)$ *and all initial conditions* $(x^0, w^0) \in \mathbb{R}^n_+ \times \mathbb{R}_+$*, the solution* (x, u) *of* (3.22) *has properties* (1)–(3) *of Theorem 3.1 and furthermore the integrator state* $w(t)$ *converges to* $r/G(1)$ *as* $t \to \infty$*.*

We provide some comments on Theorem 3.6, which is proven in Coughlan and Logemann (2009, Theorem 3.2) (see also Coughlan (2007)).

Remark 3.7. (i) Although the conclusions (1)–(3) of Theorem 3.6 are the same as those in Theorem 3.1, there is a crucial difference in the hypotheses of these theorems. Specifically, in Theorem 3.6 the desired reference value r is not completely free: it is constrained by the steady–state gain $G(1)$ and input bound U by the requirement that $r < G(1)U$. This is not unreasonable; in the presence of no control, population density is declining. If the upper limit on the number of new arrivals U is too low, or alternatively, the chosen reference r is too high, then the observations of the population cannot reach r by restocking alone. We comment further that, mathematically, this limitation is not unique to integral control. A consequence of the model under consideration (in particular equation (3.6)) is that if $u(t)$ is bounded from above by U then *any* restocking scheme cannot lead to the eventual observations ever being larger than $G(1)U$. If $r > G(1)U$ then the observations *cannot* asymptotically reach r by restocking alone.

(ii) As with Theorem 3.1, Theorem 3.6 is a low–gain result and provides the upper bound $1/|\gamma|$ for the gain g that will ensure convergence. It is shown in Coughlan (2007) that $-\infty < \gamma \leq \frac{-G(1)}{2}$. The parameter γ can be estimated numerically from its definition (3.23) although this may not always be straightforward. If **(A1)** and **(A2)** hold and if b and c^T are nonnegative then

$$\kappa := \frac{2}{G(1) + 2|G'(1)|} \leq \frac{1}{|\gamma|}\,, \tag{3.24}$$

where G' denotes the derivative of G. The constant κ is much easier to compute than γ and a derivation of (3.24) is given in Appendix A.1. Consequently, under the assumptions **(A1)** and **(A2)**, every gain $g \in (0, \kappa)$ is a "regulating gain" in the sense that conclusions (1)–(3) of Theorem 3.1 hold for (3.22).

Example 3.8. Consider a planting programme to raise levels of the savannah grass *Setaria incrassata* in the presence of heavy grazing. O'Connor (1993) contains matrix PPMs of *Setaria incrassata* where the population is partitioned into five stage–classes according to tuft circumference in cm. The specific divisions are given in (O'Connor, 1993, Table 2). The matrix we use is the average over four years (O'Connor, 1993, p.125, Table 3, first row). We control the second stage–class, plants of tuft diameter 11–20cm, and observe the total density of the all plants with tuft diameter greater than 11cm, that is, stages two to five. The matrix A, control vector b and observation vector c^T are thus given by

$$A = \begin{bmatrix} 0.5925 & 0.5900 & 0.5825 & 0.8100 & 4.5650 \\ 0.2075 & 0.3775 & 0.2475 & 0.4675 & 0.1675 \\ 0.0050 & 0.1250 & 0.4225 & 0.1850 & 0.2625 \\ 0 & 0 & 0.0850 & 0.2750 & 0.1225 \\ 0 & 0 & 0 & 0.0325 & 0.6600 \end{bmatrix}, \quad b = \begin{bmatrix} 0 \\ 1 \\ 0 \\ 0 \\ 0 \end{bmatrix}, \quad c^T = \begin{bmatrix} 0 & 1 & 1 & 1 & 1 \end{bmatrix}. \tag{3.25}$$

Figure 3.5 (a) demonstrates the results of the filtered integral control system (3.22) for different U and also the original integral control system (3.10). Here U denotes the *maximum* number of individuals that can be planted each year. From a random initial population distribution with total density 200 the goal is to raise the total measured population density to 800. In this example, $G(1) = 8.1081$ and so for fixed $r = 800$ the condition $r < G(1)U$ necessitates that U satisfies

$$\frac{r}{G(1)} = 98.6673 < U,$$

for the conclusions of Theorem 3.6 to hold. As expected, therefore, for $U = 50$ the observation does not reach the reference. As A, b and c^T are nonnegative we can use the constant κ in (3.24) as an upper bound for a regulating gain g which gives

$$\kappa = \frac{2}{G(1) + 2|G'(1)|} = \frac{2}{8.10 + 2 \times 126.42} = 0.0077.$$

We thus take $g = 0.0076 < \kappa$. Figure 3.5 (b) contains the resulting filtered input signals $\phi(w(t))$ for each U and the unfiltered signal $u(t)$ given by (3.9). We see that the linear feedback system (3.10) exhibits a large transient amplification, but also that the tracking takes longer and there is larger subsequent undershoot. Observe that here each filtered signal is truncated at U and that as U gets larger both the input and the observed population density behave more like the linear case as the filter effect is reduced.

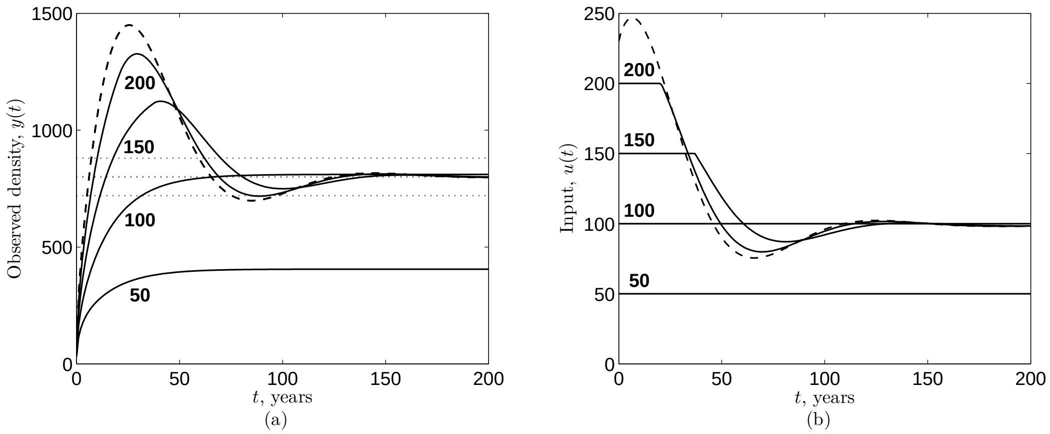


Figure 3.5: Integral control with filtered input (3.22) applied to the savannah grass matrix PPM of Example 3.8 with different U values. (a) Observations in solid lines, labelled with the corresponding U value. The dashed line is the observation subject to the unfiltered integral control system (3.10). The dotted lines are the reference $r = 800$ and $r \pm 10\%$. (b) Filtered input signal $u(t) = \phi(w(t))$ in solid lines labelled with corresponding U value. The dashed line is the unfiltered input generated by (3.9).

Remark 3.9. We comment that Theorem 3.6 can be extended to the feedback system (3.22) with the nonlinear filter ϕ replaced by other nonlinearities. Details are contained in Appendix A.3. For example, if ϕ is replaced by a function that grows sublinearly then there are increasingly diminishing returns from larger input signals. In the context of a plant population, if the control term $bu(t)$ denotes sowing seeds, then at high densities the proportion of seeds that become plantlings may not depend linearly on the number of seeds sown owing to density–dependence effects. Such an effect can be modelled by a suitable choice of ϕ in (3.22).

3.3 *How small does the gain g in the feedback strategy* (3.9) *need to be?*

Here we discuss the design parameter g in more detail . We seek to explain its role and how suitable g can be chosen or estimated. Finally, we include another feature in the integral control model which computes g adaptively, circumventing the need to choose it altogether **(P3)**.

The choice of g affects the performance of integral control. As a tuning parameter; a larger g usually corresponds to a faster response, which is sometimes desirable. As the next precautionary example demonstrates, however, choosing g too large may result in failure of the control objective.

Example 3.10. We revisit the wild boar matrix PPM considered in Example 3.2. For fixed A, b, c^T, x^0, u^0 and r as in that example we project the filtered integral control system (3.22) with $U = 200$ for increasing gains $g = 0.05, 0.3, 0.6$ and have plotted the results in Figure 3.6. We see that the observations oscillate around r with greater magnitude as g increases, and fails to converge to the reference for $g = 0.6$. Note that the filtered input $u(t)$ is truncated at both zero and U.

Recall the characterisation from (3.13) of which gains g result in convergence of the observations– those such that $\rho(A_g) < 1$. Describing the dependence of $\rho(A_g)$ on g analytically is, in general, intractable. It is of course true that for each candidate $g > 0$, $\rho(A_g)$ can be computed numerically, but this does not provide a systematic method of finding how large g can be, or the qualitative behaviour of the resulting dynamics. Notwithstanding the above, the *root locus* method developed by Evans (1948, 1950)

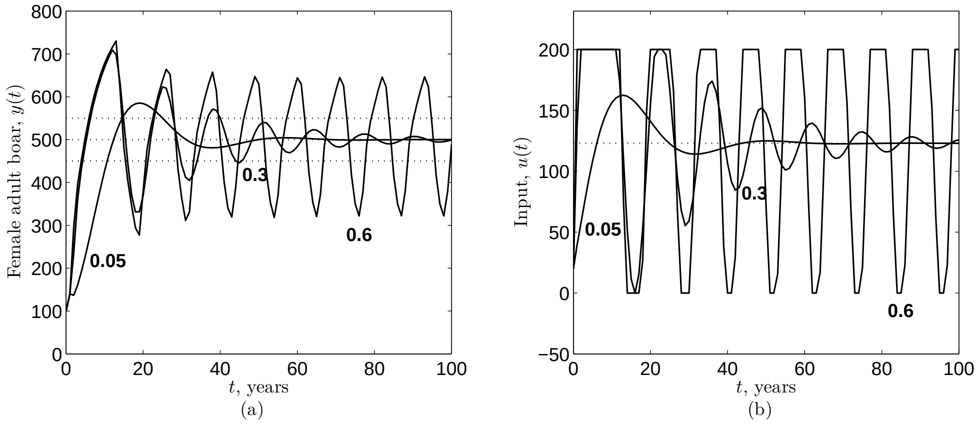


Figure 3.6: Integral control with filtered input (3.22) applied to the wild boar matrix PPM of Example 3.2 with different gain parameters. See Example 3.10. Each line is labelled with its gain g. (a) Observations. The dotted lines are the reference $r = 500$ and $r \pm 10\%$. (b) Filtered input signals with $U = 200$. The dotted line is $r/G(1)$.

is a graphical method of describing how the eigenvalues of A_g in this instance (more precisely, the *poles of the closed–loop system* (3.13)) change with the parameter g. This powerful technique can be used to choose g in such a manner that both of the conclusions of Theorem 3.1 apply *and* qualitative and quantitative properties of the resulting dynamics are specified. Many textbooks provide a modern treatment of the root locus method and we refer the reader to Franklin et al. (1994, Chapter 4) for more information.

Regarding model uncertainty, we comment that the choice of g is robust to model uncertainty in the following sense. If $g^* > 0$ is such that $\rho(A_{g^*}) < 1$ then there exists $\varepsilon > 0$ such that $\rho(\tilde{A}_{g^*}) < 1$ for all $\tilde{A}_{g^*}$ with $\|A_{g^*} - \tilde{A}_{g^*}\| < \varepsilon$. In words, if g^* is a regulating gain for a given A_g then g^* is a regulating gain for all $\tilde{A}_{g^*}$ "close enough" to A_{g^*}. Recalling that A_g depends on A, b, c^T and g, this amounts to model uncertainty in A, b and c^T that is "small enough". The terms "close enough" and "small enough" can be precisely quantified by appealing to stability radius arguments (Hinrichsen and Pritchard, 1986a,b).

The presence of the nonlinear filter ϕ in the integral control system (3.22) prevents the root locus method from being applied here and the proof of Theorem 3.6 is more subtle. Here it is very difficult in general to find an exact expression for the largest gain that results in convergence, and so in order to apply Theorem 3.6 a positive lower bound for $1/|\gamma|$ is required. The constant κ in (3.24) is such a bound in the (usual) case where A, b and c^T are nonnegative. However, the same problem arises as with the precomputed control (3.8) because the formula for κ depends on the model data A, b and c^T. Although γ and κ are robust to model uncertainty in a similar sense to g as described above (that is, "small" perturbations to A, b and c^T can be tolerated), in the presence of *severe* uncertainty in A, b and c^T, using (3.24) may not give a correct lower bound for the "true" $1/|\gamma|$.

A different approach, therefore, may be desirable for choosing g. The next method we present is an example of *adaptive control* (Landau, 1979; Sragovich, 2006; Astolfi et al., 2008), where in this instance the parameter g is determined via a suitable adaptation rule. That is, we allow the gain parameter g also to change with time, determined by a dynamical system included in the feedback loop. Specifically, we set

$$g(t) = \frac{1}{h(t)}, \quad h(t+1) = h(t) + |r - y(t)|, \quad t = 0, 1, 2, \dots ,$$

which yields the adaptive integral control system

$$\left.\begin{aligned} x(t+1) &= Ax(t) + bu(t)\,, & x(0) &= x^0\,,\\ w(t+1) &= w(t) + (h(t))^{-1}(r - c^T x(t))\,, & w(0) &= w^0\,,\\ h(t+1) &= h(t) + |r - y(t)|\,, & h(0) &= h^0\,,\\ u(t) &= \phi(w(t))\,. \end{aligned}\right\} \quad t = 0,1,2,\dots\,. \tag{3.26}$$

Figure 3.7 contains a diagram of the arrangement in (3.26). The main result of this section is Theorem 3.11 below, which is a special case of a result in Logemann and Ryan (2000), and is an adaptive version of Theorem 3.6 which obviates the need to choose a gain parameter g.

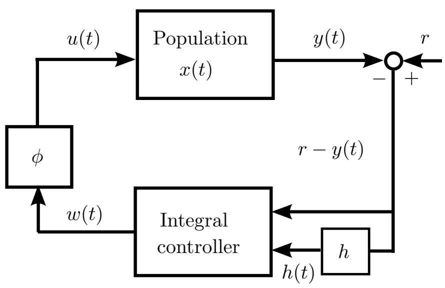


Figure 3.7: Block diagram of the adaptive feedback system (3.26). The constant gain parameter g is replaced by a dynamic signal $h(t)$ which itself is determined by the difference $r - y(t)$.

Theorem 3.11. *Assume that the linear system* (3.5) *satisfies assumptions* **(A1)** *and* **(A2)**. *Then, for every $U > 0$, every $r \in (0, G(1)U)$ and all initial conditions $(x^0, w^0, h^0) \in \mathbb{R}^n_+ \times \mathbb{R}_+ \times (0, \infty)$, the solution (x, u, h) of* (3.26) *has properties* (1)–(3) *of Theorem 3.1, the integrator state $w(t)$ converges to $r/G(1)$ as $t \to \infty$ and additionally*

(4) *the non–increasing gain $g(t) = 1/h(t)$ converges to a positive limit depending on (x^0, w^0, h^0) as $t \to \infty$.*

Remark 3.12. (i) Theorem 3.11 is remarkable because it ensures that the integral control system (3.26) achieves the desired control objective in the presence of *very* little information. The reference r, observations $y(t)$ and assurance that $r < G(1)U$ are required, but knowledge of A, b, c^T, x^0 and crucially a suitable gain $g > 0$ is not!

(ii) As with Theorem 3.6, the version of Theorem 3.11 presented is a special case of a more general result, where the filter ϕ can be replaced by other functions. More details are contained in Appendix A.3.

Example 3.13. Theorem 3.11 is applied to the wild boar model of Example 3.2. For the same A, b, c^T as in that example, but with $r = 200$, the adaptive integral control system (3.22) for gains g determined adaptively via (3.26) is projected for three different (x^0, w^0, h^0) triples. The results are plotted in Figure 3.8. Here the convergence of the observations to the reference ensured by Theorem 3.11 is slow, note the log x–axes in the figure. This is because in the adaptive control scheme (3.26) the gain $g(t) = 1/h(t)$ always decreases and can become small very quickly resulting in sluggish performance. Recall, however, that the control scheme has no knowledge of A, b or c^T, only that $\rho(A) < 1$, $G(1) > 0$ and that $r < G(1)U$.

3.4 *Can the rate of convergence of the observations to the reference be improved?*

By adding a (P)roportional part to the (I)ntegral control feedback strategy (3.9) the resulting rate of convergence of the observations to the reference can be increased **(P4)**.

So far we have been using integral control to move the equilibrium of a declining model to a chosen non–zero equilibrium. As mentioned in the introduction, integral control is just one part of PID–control. Loosely speaking, the observations resulting from a PI control strategy converge faster to the reference.

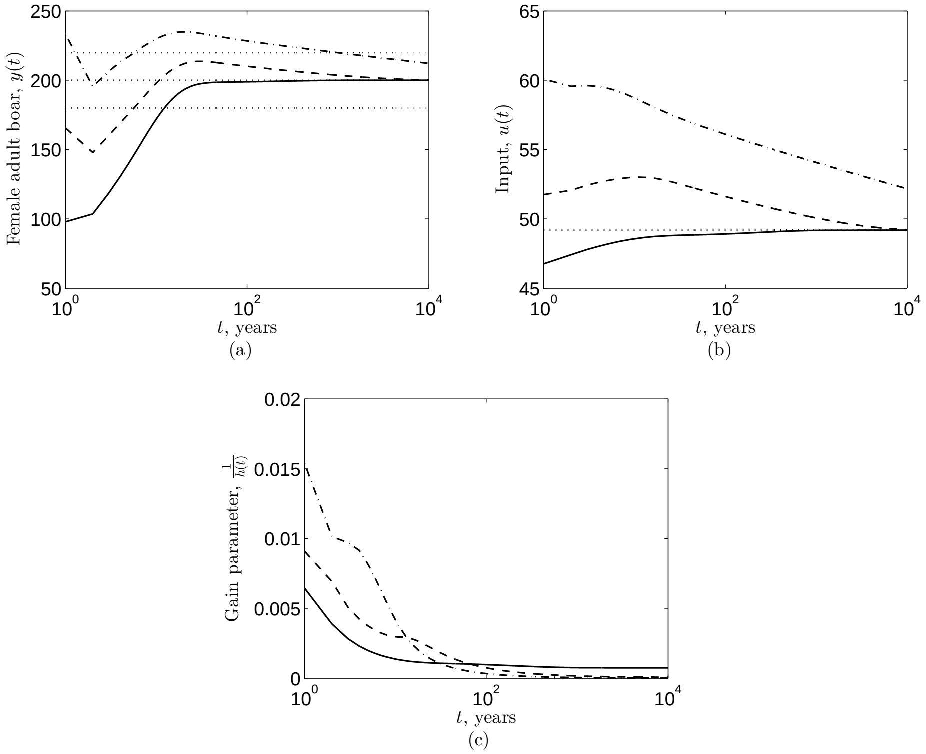


Figure 3.8: Adaptive integral control (3.26) applied to the wild boar matrix PPM of Example 3.2 with different initial triples (x^0, w^0, h^0). See Example 3.13. In each plot the solid, dashed and dashed–dotted lines are corresponding simulations. (a) Observations. The dotted lines are the reference $r = 200$ and $r \pm 10\%$. (b) Filtered input signals and limiting input $r/G(1)$ in dotted line. (c) Adaptive gain parameters $g(t) = \frac{1}{h(t)}$.

We proceed to give the details. In the first instance, we replace the integral control system (3.10) by

$$\left.\begin{aligned} x(t+1) &= Ax(t) + bu(t), & x(0) &= x^0, \\ w(t+1) &= w(t) + g(r - c^T x(t)), & w(0) &= w^0, \\ u(t) &= w(t) + g(r - c^T x(t)), & & \end{aligned}\right\} \quad t = 0, 1, 2, \dots. \tag{3.27}$$

In (3.27), w is the integrator state and u is the control, now given by

$$u(t) = w^0 + g \sum_{j=0}^{t} (r - y(j)), \quad t = 0, 1, 2, \dots. \tag{3.28}$$

The difference between (3.9) and (3.28) is that in the latter, at each time–step t, $u(t)$ depends on the *current* observation error $r - y(t)$ and not just the *previous* errors. In our original system (3.10) we had $u(t) = w(t)$, that is, the control was simply an integrator– I control. We now compute u by adding to w the current error $r - y(t)$. The motivation for using such a control strategy is that the current error $r - y(t)$ acts as a (P)proportional part which increases the rate of convergence.

As we are considering population models, where $x(t)$ needs to be nonnegative, for the model (3.27) to be meaningful we require the constraint that $A - gbc^T$ is componentwise nonnegative, which we note may not always be satisfied. However, whenever this is the case, the conclusions of Theorem 3.1 and Theorem 3.11 hold for the integral control system (3.27) with small enough gain g and suitably modified adaptive case respectively. The conclusions of Theorem 3.6 also hold (see Coughlan (2007)), but with γ in (3.23) replaced by

$$\gamma_0 := \sup_{q \geq 0} \left\{ \inf_{\theta \in [0, 2\pi)} \mathrm{Re} \left[\left(q + \frac{\mathrm{e}^{i\theta}}{\mathrm{e}^{i\theta} - 1} \right) G(\mathrm{e}^{i\theta}) \right] \right\} .$$

Again, we demonstrate in Appendix A.1 that under assumptions **(A1)** and **(A2)** and if b and c^T are nonnegative then

$$\kappa_0 := \frac{2}{G(1) + 2|G(1) + G'(1)|} \leq \frac{1}{|\gamma_0|} , \tag{3.29}$$

so that the conclusions of the theorem hold for the system (3.27) for every gain g such that $g \in (0, \kappa_0)$. Furthermore, we show that $\kappa < \kappa_0$, so that certainly the range of regulating gains for (3.27) is not smaller than that for (3.10).

The rate of convergence of the observations to the reference can be tuned even further in the linear integral control case by making the following alteration. We consider now the feedback scheme

$$\left.\begin{aligned} x(t+1) &= Ax(t) + bu(t), & x(0) &= x^0, \\ w(t+1) &= w(t) + g(r - c^T x(t)), & w(0) &= w^0, \\ u(t) &= w(t) + k(r - c^T x(t)), & & \end{aligned}\right\} \quad t = 0, 1, 2, \ldots . \tag{3.30}$$

The term $k(r - c^T x(t))$ is a proportional feedback and the parameter $k > 0$ is called the proportional feedback gain. We note that the integral control system (3.27) is a special case of (3.30) where $k = g$, but in general they need not be the same. Although the parameter k introduces another choice that has to be made by the modeller, its inclusion often results in faster convergence of the observations to the reference as Example 3.15 demonstrates. Our main result for PI control is Theorem 3.14 below which is proven in Appendix A.4.

Theorem 3.14. *Assume that the linear system* (3.5) *satisfies assumptions* **(A1)** *and* **(A2)** *and assume that $k > 0$ is such that $A - kbc^T$ is nonnegative with b and c^T also assumed nonnegative. Then there exists $g^* > 0$, which depends on k, such that for all $g \in (0, g^*)$, every $r > 0$ and all initial conditions $(x^0, w^0) \in \mathbb{R}^n_+ \times \mathbb{R}_+$, the solution (x, u) of* (3.30) *satisfies properties* (1)–(3) *of Theorem 3.1 and additionally the integrator state $w(t)$ converges to $r/G(1)$ as $t \to \infty$.*

Example 3.15. We compare the rates of convergence of the observations to the reference of the integral control systems (3.10), (3.27) and (3.30) when applied to the wild boar model of Example 3.2. The results are plotted in Figure 3.9. The systems (3.10) and (3.27) both have the same gain parameter $g = 0.12$, as in Example 3.2. We see that the observations of (3.27) converges faster and in a less oscillatory manner than those of (3.10). For the PI system (3.30) we take increasing proportional gain parameter $k = 0.2, 0.3$ and $k = 0.4$ and note the progressively faster convergence of the observations to the reference.

3.5 *Can integral control be applied to other population models?*

Here we demonstrate that integral control can be applied to (I)ntegral (P)rojection (M)odels and that the results on integral control for matrix PPMs from Sections 3.2 and 3.3 extend to IPMs. We also comment on how certain spatially structured models fit into an integral control framework **(P5)**.

IPMs are a relatively recent approach to population modelling, introduced in Easterling et al. (2000). Since their inception several models have been published in, for example Ellner and Rees (2006); Childs et al. (2003); Rees and Ellner (2009) and Ozgul et al. (2010). We refer the reader to Easterling et al. (2000), or the tutorial paper Briggs et al. (2010), for full details and only give a brief overview here. Typically an IPM takes the form

$$n(\xi, t+1) = \int_{s \in \Omega} k(s, \xi) n(s, t) \, ds, \quad n(\xi, 0) = n_0(\xi), \quad \xi \in \Omega, \quad t = 0, 1, 2, \ldots . \tag{3.31}$$

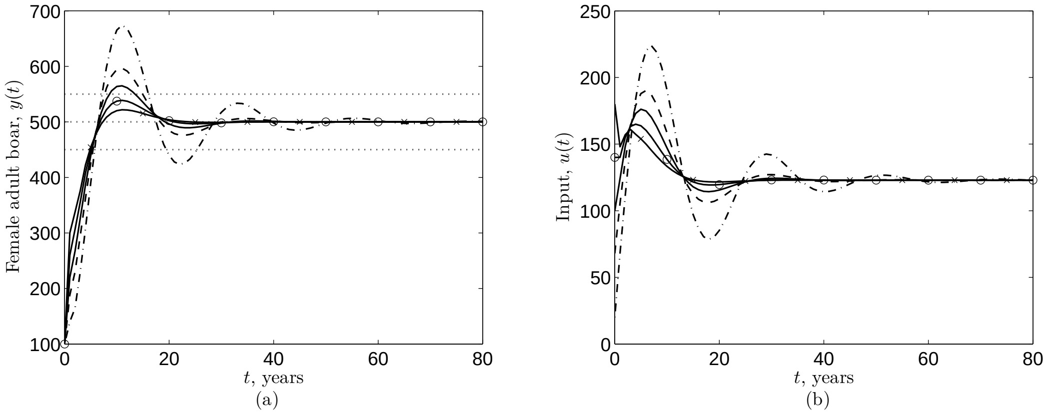


Figure 3.9: Integral control (3.10), integral control with proportional feedback (3.27) and PI system (3.30) applied to the wild boar matrix PPM of Example 3.2. See Example 3.15. (a) Observations. The dotted lines are the reference $r = 500$ and $r \pm 10\%$. (b) Inputs. In both (a) and (b): the dashed–dotted line is the original system (3.10) with $g = 0.12$, the dashed line is the system (3.27) with $g = 0.12$ and the solid, solid–circled and solid–crossed are the PI system (3.30) with increasing $k = 0.2, 0.3$ and 0.4 respectively.

Here $n(\xi, t)$ denotes the population at stage $\xi \in \Omega$ and time–step t, where Ω is the range of size or stage–classes and is usually an interval of real numbers (although more general sets are permitted, see Ellner and Rees (2006)). For each fixed t, $n(\xi, t)$ is a function of ξ. The function k is called a projection kernel and describes the life history parameters of survival, growth and fecundity of the population.

The model (3.31) can be written in the form (3.1), where A now denotes the operator

$$A : L^1(\Omega) \to L^1(\Omega), \quad (Av)(\xi) = \int_{s \in \Omega} k(s, \xi) v(s)\, ds, \tag{3.32}$$

where $L^1(\Omega)$ is the space of Lebesgue measurable functions (see, for example, Evans (2010, p. 647)) with finite L^1 norm

$$L^1(\Omega) = \left\{ f : \Omega \to \mathbb{R} \ : \ f \text{ Lebesgue measurable and} \int_{x \in \Omega} |f(x)|\, dx < \infty \right\}.$$

In order to convert the IPM (3.1) (where A is now given by (3.32)) into a controlled and observed system (3.5) we need to introduce appropriate control vector b and observation vector c (the superscript ^{T} is omitted as we are no longer considering matrix transposition).

Example 3.16. Suppose that for an IPM, $\Omega = [\alpha, \beta]$, the interval from the minimal size α to the maximal size β. In such a framework the control action is a mapping $\mathbb{R} \to L^1(\Omega)$ and a suitable choice for b is a function in $L^1(\Omega)$ so that the control term $bu(t)$ in (3.5) is b multiplied by the scalar $u(t)$. To model the distribution of new individuals arriving uniformly between stage–classes ξ_1 and ξ_2 with $\alpha \le \xi_1 < \xi_2 \le \beta$ we define b by

$$b(s) = \begin{cases} \dfrac{1}{\xi_2 - \xi_1}, & s \in [\xi_1, \xi_2], \\ 0, & \text{otherwise.} \end{cases} \tag{3.33}$$

The function b distributes new arrivals uniformly between ξ_1 and ξ_2. In some applications, it may be more realistic that the distribution of new arrivals is not uniform, and perhaps centered around some point between ξ_1 and ξ_2. Such a control vector represents a 'smoother' version of b in (3.33). There are many such functions with this property. The quartic function

$$b'(s) = \begin{cases} \dfrac{30}{(\xi_2 - \xi_1)^5} (s - \xi_1)^2 (s - \xi_2)^2, & s \in [\xi_1, \xi_2], \\ 0, & \text{otherwise,} \end{cases} \tag{3.34}$$

is one example. The scaling of b' is chosen so that b' integrates to one. For matrix PPMs the observation vectors we consider are row vectors. The equivalent of a row vector in the IPM context is a linear mapping $L^1(\Omega) \to \mathbb{R}$. For example, the mapping

$$v \mapsto cv := \int_{\xi_1}^{\xi_2} v(s)\, ds, \tag{3.35}$$

models the measurement of the population density of v between stage–classes ξ_1 and ξ_2. When $\Omega = [\alpha, \beta]$ and $\xi_1 = \alpha$, $\xi_2 = \beta$ then c in (3.35) measures the entire population density.

Mathematically, PPMs and IPMs are very similar, although the latter involve some extra technicalities. Theorem 3.17 is the main result of this section and demonstrates that our main results for matrix PPMs carry over to IPMs. Theorem 3.17 is a combination of special cases of results originally proven in Coughlan and Logemann (2009); Coughlan (2007) and Logemann and Ryan (2000).

The two key assumptions **(A1)** and **(A2)** in the matrix PPM case captured the properties that the uncontrolled population is in asymptotic decline and that the control, model and observation are chosen so that the steady–state gain is non–zero respectively. The same assumptions are required for IPMs although the formulation is slightly more technical: specifically, let X denote a Banach space,

(A1′) the bounded linear operator $A : X \to X$ has $\rho(A) < 1$,

(A2′) the operators $A : X \to X$, $b : \mathbb{R} \to X$ and $c : X \to \mathbb{R}$ are all bounded and such that $c(I-A)^{-1}b > 0$.

We comment that assumption **(A1′)** can be checked numerically and assumption **(A2′)** generally holds for the IPMs presented here. In more detail, for $\Omega = [\alpha, \beta]$ the space $L^1(\Omega)$ is a Banach space and for "reasonable" kernels k, (for instance, if k is square integrable) the operator A in (3.32) is compact. Compact operators can be uniformly approximated by finite dimensional operators, so the spectral radius of A can be estimated by computing the spectral radii of a sequence of finite dimensional approximations of A. More precisely, if $(A_n)_{n=1}^{\infty}$ is a matrix sequence that approximates A uniformly, then by, for example, Degla (2008, Theorem 2.1), the spectral radii $\rho(A_n)$ converge to $\rho(A)$.

Assumption **(A2′)** means that a constant positive input signal eventually gives rise to a positive observation. Alternatively, suppose that the controlled and observed IPM is given by A (for reasonable kernels k), input b and observation c as in (3.32), (3.33) and (3.35) respectively. If A, b and c are uniformly approximated by A_n, b_n and c_n then

$$G_n(1) := c_n(I - A_n)^{-1}b_n \to c(I-A)^{-1}b = G(1), \quad \text{as } n \to \infty\,,$$

and so the computable steady–state gain of A_n,b_n and c_n converges to that of A, b and c.

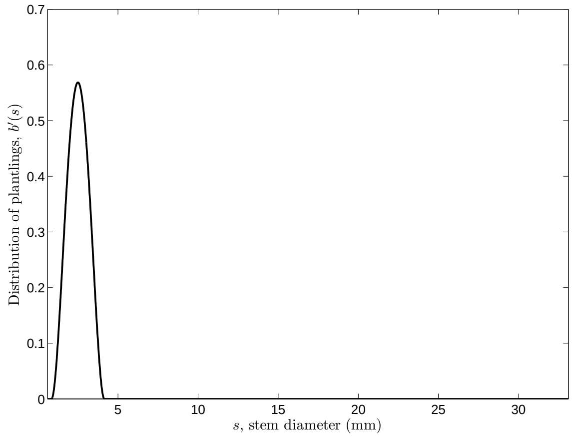
Theorem 3.17. *Given the controlled and observed projection system* (3.10) *in the IPM case, then under assumptions* **(A1′)** *and* **(A2′)** *the conclusions of Theorem 3.1 hold. If additionally the input bound* $U > 0$ *and reference* $r > 0$ *are such that* $r \in (0, G(1)U)$ *then the conclusions of Theorems 3.6 and 3.11 apply to the IPM versions of* (3.22) *and* (3.26) *respectively.*

For a proof of the above result we refer the reader to Coughlan and Logemann (2009); Coughlan (2007) for the first two claims and Logemann and Ryan (2000) for the third.

Example 3.18. We consider an IPM for platte thistle (*Cirsium canescens*) based on that from Rose et al. (2005), discussed also in Briggs et al. (2010). Here the stages are structured according to stem diameter; a continuous variable assumed to take values between ~ 0.6mm and ~ 33mm. The distribution of plants of stage ξ at time t is denoted by $n(\xi, t)$. We have altered some of the parameters in the model from those in Rose et al. (2005) so that the ambient population is in asymptotic decline.

To supplement this population we suppose that individuals of stem diameter centered around 2.5mm are planted at each step, distributed by b' from (3.34) with $\xi_1 = 2.5 - \mathrm{e}^{0.5}$mm and $\xi_2 = 2.5 + \mathrm{e}^{0.5}$mm. The distribution of new plants is plotted in Figure 3.10.

Figure 3.10: Graph of function b' describing distribution of new plants at each time–step of IPM Example 3.18. Here $\xi_1 = 2.5 - e^{0.5}$ and $\xi_2 = 2.5 + e^{0.5}$.



The observation $y(t)$ of the population at each time–step is the total density of all plants with diameter between 22mm and 30mm, described by

$$y(t) = (cn)(t) = \int_{22}^{30} n(s,t)\, ds.$$

From a random initial population of total density 10 we seek to raise the total density of thistles with diameter in the range 22mm–30mm to $r = 40$. In order to simulate the model we discretise the IPM; which we do so via a finite element (FE) method, a standard technique in numerical analysis. Such a scheme produces a matrix equation that approximates the controlled and observed IPM, but is different from one obtained by parameterising a PPM model. The details of the approximations are contained in Appendix A.5. We assume that the the input filter ϕ is present, with input bound $U = 15$, and since $G(1) = 3.3196$, in order for the results of Theorem 3.17 to apply we require

$$r < G(1)U = 49.7\,.$$

The results of the simulations are plotted in Figure 3.11. We see that, as expected, each control scheme achieves the desired control objective.

We conclude this section with two remarks on other directions in which integral control can be developed.

Remark 3.19. Integral control can be developed for population models that contain a spatial component. The theoretical results we have drawn upon and derived here are predicated on the underlying population model being density–independent (that is, linear) and provided that linearity is preserved in the presence of spatial dynamics, then integral control is still applicable. It is beyond the scope of the present contribution to give comprehensive details for such situations but we do consider two examples. The first is a controlled and observed matrix metapopulation model (for example Pulliam (1988) or more recently Roy et al. (2005)), so that a population changes over time and across N discrete patches, for integer N. The stage–structured population in the i^{th} patch at time–step t is denoted $x_i(t)$ and has dynamics described by

$$x_i(t+1) = A_i x_i(t) + \sum_{j=1}^{N} D_{ij} x_j(t) + b_i u(t), \quad x_i(0) = x_i^0, \quad t = 0, 1, 2, \dots\,, \tag{3.36}$$

for $i \in \{1, 2, \dots, N\}$. Here A_i describes the survival and recruitment of the i^{th} patch, D_{ij} are dispersal matrices, describing the movements of individuals to patch i from patch j and b_i is the control vector of the i^{th} patch. Spatial inhomogeneity is incorporated when the vital rates and dispersal rates vary across patches. The model (3.36) can be reformulated in the form (3.5) by concatenating the population

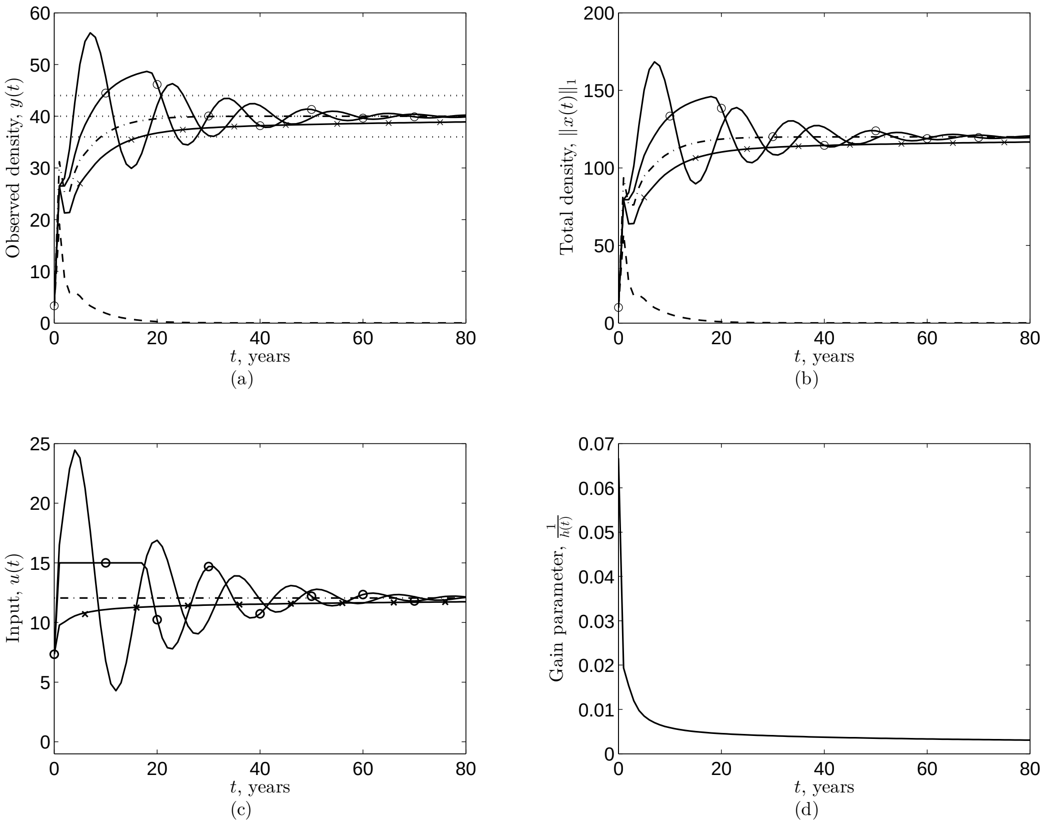


Figure 3.11: Integral control applied to the (discretisation of the) platte thistle IPM of Example 3.18. (a) Observations. (b) Total population densities. (c) Inputs. (d) Adaptive gains. In (a)–(c) the solid lines denote the original integral control system (3.10), the solid–circled lines are the filtered integral control system (3.22) and the solid–crossed lines are the adaptive integral control system (3.26). The dashed–dotted line is the precomputed control and the dotted lines denote the reference $r = 40$ and $r \pm 10\%$. The dashed lines in (a)–(b) denote projections from the uncontrolled model. Each projection is from the same random initial population distribution. Here $r = 40$, $U = 15$ and $g = 0.25$.

vectors and patch matrices as

$$x(t) := \begin{bmatrix} x_1(t) \\ x_2(t) \\ \vdots \\ x_N(t) \end{bmatrix}, \quad A := \begin{bmatrix} (A_1 + D_{11}) & D_{12} & \dots & D_{1N} \\ D_{21} & \ddots & & \vdots \\ \vdots & \ddots & \ddots & D_{N-1N} \\ D_{N1} & \dots & D_{NN-1} & (A_N + D_{NN}) \end{bmatrix}, \quad b := \begin{bmatrix} b_1 \\ b_2 \\ \vdots \\ b_N \end{bmatrix}, \tag{3.37}$$

and by defining an observation $y(t)$ as some linear combination of the states $y(t) = c^T x(t)$ as usual. It is important to note that the D_{ij} may not be componentwise nonnegative, as they describe both movement in to and out of a given patch and so therefore A in (3.37) may have negative components. However, the nonnegativity assumed in **(A1)** is not required for integral control, only that $\rho(A) < 1$. Assumption **(A2)** is unchanged, and when these assumptions hold for the above A, b and c^T then integral control is applicable and the results we have presented carry over. As mentioned in Section 3.1, full knowledge of A_i, D_{ij} is not required for these assumptions to hold.

The second example is a linear, integro–difference model (for examples in ecology, see Kot (1992) or Kot et al. (1996) and the references therein). A single stage–structured population over a (possibly inhomogeneous) spatial domain Ω at time–step t and position $\xi \in \Omega$ is denoted by $n(\xi, t)$ and has dynamics given by

$$\left.\begin{aligned} n(\xi, t+1) &= \int_{s\in\Omega} k(\xi, s) R n(s,t)\, ds + b(\xi)u(t)\,, \quad n(\xi, 0) = n_0(\xi), \\ y(t) &= \int_{\Omega_1} \begin{bmatrix} 1 & 1 & \dots & 1 \end{bmatrix} n(s,t)\, ds\,, \end{aligned}\right\} \quad t = 0, 1, 2, \dots\,, \tag{3.38}$$

In (3.38), R is a matrix that models survival and recruitment of the population, n_0 denotes the initial population distribution, $k = k(\xi, s)$ is a dispersal kernel which is a probability distribution describing the probability that an individual from position s disperses to position ξ at each time–step and the function $b = b(\xi)$ describes the distribution of new individuals at position ξ. The observation $y(t)$ has been chosen as the number of individuals in the region $\Omega_1 \subseteq \Omega$, although of course other observations are permitted. Similarly to the IPM (3.31), (3.38) can be reformulated as (3.5), although we do not give the details here.

Remark 3.20. Further developments of integral control allow regulation of more than one observation and with access to more than one management action at each time–step. For example, suppose that we seek to regulate *both* the total population abundance *and* the abundance of a given single stage–class, and we can replenish more than one stage–class (or combination of stage–classes) independently. This leads to a framework called *multi–input, multi–observation* in control engineering and conceptually the extension from the *single–input, single–observation* case is usually straightforward, although mathematically there are often additional difficulties to overcome. That said, integral control feedback systems have been designed where at each time–step t, m control actions are made and p observations are recorded for positive integers m and p; for example by Ke et al. (2009). The reference is now a vector of chosen values $\mathtt{r} \in \mathbb{R}^p$. However, existing results do not address integral control where additionally componentwise nonnegativity has to be preserved; clearly a requirement for meaningful population models. Combining these twos ideas is seemingly not straightforward. One immediate issue is that not every nonnegative reference vector can be a target for management. In our example considered above, obviously the former observation (total population abundance) shall always be larger than the latter (abundance of a single stage–class). Such a constraint must therefore also be present in the choice of reference. We comment that integral control that preserves nonnegativity in the multi–input, multi–observation case is the subject of ongoing research.

3.6 How the solutions to (P1)–(P5) interact

The solutions proposed to problems **(P1)**–**(P5)** interact as follows. Robustness to model uncertainty **(P1)** *(i)* is encapsulated in assumptions **(A1)** and **(A2)**, which are necessary and sufficient conditions for low–gain integral control and are hence assumed throughout. The same is true of the infinite–dimensional versions of these assumptions **(A1′)** and **(A2′)**. Thus the solutions to **(P2)**–**(P5)** include this same robustness to model uncertainty. The material presented in addressing **(P2)**, **(P3)** and **(P5)** is cumulative, so our solution to **(P3)** (adaptive gain selection) incorporated the solution to **(P2)** (filtering the input signal). We addressed problem **(P4)**, namely that of increasing the rate of convergence of the observations to the reference, by including a (P)roportional controller to augment the (I)ntegral controller. For simplicity our main result of Section 3.4, Theorem 3.14, only considered the linear integral control system (3.10). However, Theorems 3.6, 3.11 and 3.17 can all be extended to the PI feedback system (3.27) (where the proportional k and integral gains g are equal). It is possible to extend versions of all the theorems presented to incorporate additive observation errors and additive activation errors (**(P1)** *(ii)* and *(iii)* respectively). The proportional observation errors (3.17) are trickier to incorporate into the solutions to **(P2)**–**(P5)**, and a treatment of such is beyond the scope of this contribution. However, appealing to techniques such as λ–tracking (Ilchmann, 1991; Ilchmann and Ryan, 1994) and funnel control (Ilchmann et al., 2002) would provide insight in this direction.

4 Discussion

We have introduced integral control as a potential tool for population management. A brief overview of the method has been given, which seeks to motivate both the necessity of integral control for robust population management via restocking and indeed further how integral control is suitable for such a task. Sections 2 and 3 contain a verbal and mathematical "road map" respectively of how integral control is applied. Although well–established in control engineering and, as mentioned in the introduction, now starting to appear in the biological literature; PI control has not been applied to population management, to which we feel it is well suited. It has been suggested elsewhere in the literature that there is ample scope for using control theory in ecology (Gouzé et al., 2000; Blackwood et al., 2010) but often it seems that the focus is on optimal control (Lenhart and Workman, 2007). As mentioned in Section 2.1, the trade–off between performance and robustness has produced an unfortunate discord between theory and practice, so much so that Safonov and Fan (1997) write (of optimal control) "By 1975, the much lamented gap between academic theory and engineering practice in the control field had grown to prodigious proportions."

Integral control is a particular instance of feedback control, which is known to control engineers to be incredibly robust to model uncertainty. Moreover, appealing in part to recent mathematical results by the authors, the basic integral control model can be extended to meet several challenges that arise in population ecology.

Furthermore, integral control is straightforward to implement (at least theoretically) once a PPM or IPM is available. It does not suffer the so–called "curse of dimensionality" present in SDP which necessitates low–dimensional models to be realised practically. Of course population management models that use POMDPs and SDP (such as those cited in Section 2.1) treat an issue that we have omitted; namely that of managing optimally. The reason for this omission is, in part, because it is not the aim of the present manuscript. We have sought to describe a robust approach to population management via restocking. With the material presented, however, and given costs of reintroduction and observation one could easily investigate by simulation which choices of b, c^T and g (reintroductions, measurements, and gain) give rise to lowest costs or fastest responses. Such costs could also be traded off against set rewards of having certain abundances of populations.

Another important consideration is that we, to use a medical analogy, have presented a treatment of symptoms rather than a cure of the underlying condition, as managing via integral control requires that populations are restocked indefinitely to secure persistence. Such a policy is clearly infeasible in practice, at least in many cases. Although conservation biologists often rely on captive rearing, translocations and species reintroductions (Sarrazin and Barbault, 1996); methods that fit our mathematical framework, such conservation programmes are expensive, laborious and risk the welfare of endangered species. A possibly more practical approach would be to combine integral control in the short term to raise population abundances with additional conservation efforts to ensuring future population persistence, for example by improving environmental conditions. The aim might be to restock to sufficient population densities that ensure population viability; that is, the population persists unaided. In closing, it is our hope that the methods described here shall join the suite of modelling tools available to population managers.

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A Appendix

A.1 The constants γ, κ, μ_g and ν_g

• We first prove the inequality (3.24). In the proceeding arguments, for a sequence v we use the notation $\hat{v}$ to denote the Z–transform of v given by

$$\hat{v}(z) = \sum_{j=0}^{\infty} v(j) z^{-j},$$

defined for all complex z where the summation converges absolutely. The step response of the linear system (3.5) is the output of (3.5) subject to zero initial state ($x^0 = 0$) and constant input $\tilde{u} = 1$ and is given by

$$s(0) = 0, \quad s(t) = \sum_{j=0}^{t-1} c^T A^j b, \quad t = 1, 2, \ldots.$$

Assumption **(A1)** ensures that $s(t) \to G(1)$ as $t \to \infty$. Furthermore, a calculation shows that s has Z–transform

$$\hat{s}(z) = \frac{zG(z)}{z-1}, \quad z \in \mathbb{C}, \quad |z| > 1\,.$$

Under the assumptions that $A, b, c^T \geq 0$ and **(A2)** it follows that $s(t) \geq 0$ and is non–decreasing. We define the step response error

$$e(t) = s(t) - G(1), \quad t = 0, 1, 2, \ldots,$$

which is consequently non–positive, non–decreasing and converges to 0. Furthermore, the Z–transform of e satisfies

$$\frac{\hat{e}(z)}{z} = \frac{G(z) - G(1)}{z-1}, \tag{A.1}$$

for every complex z with modulus greater than one. Since G is differentiable at $z = 1$ we note that

$$\lim_{z \to 1} \hat{e}(z) = \lim_{z \to 1} \frac{\hat{e}(z)}{z} = \lim_{z \to 1} \frac{G(z) - G(1)}{z-1} = G'(1)\,. \tag{A.2}$$

As $z \mapsto \frac{\hat{e}(z)}{z}$ is continuous outside of the unit disc the above shows that we can extend $z \mapsto \frac{\hat{e}(z)}{z}$ continuously to $z = 1$ with

$$\hat{e}(1) = \frac{\hat{e}(1)}{1} = G'(1)\,. \tag{A.3}$$

We now use (A.3) and the property that $e(t) \leq 0$ for every t to show that for any complex z with modulus one,

$$\begin{aligned} -G'(1) = -\hat{e}(1) = -\sum_{k=0}^{\infty} e(k) = \sum_{k=0}^{\infty} |e(k)| \cdot |z^{-(k+1)}| \geq \left| \frac{\hat{e}(z)}{z} \right| \geq \mathrm{Re} \left(\frac{-\hat{e}(z)}{z} \right) = \mathrm{Re} \left[\frac{G(1) - G(z)}{z-1} \right] \\ = -\frac{G(1)}{2} - \mathrm{Re} \left[\frac{G(z)}{z-1} \right]. \end{aligned} \tag{A.4}$$

Rearranging (A.4) gives

$$\mathrm{Re}\left[\frac{G(z)}{z-1}\right] \geq G'(1) - \frac{G(1)}{2}, \quad \text{for all complex } z \text{ with modulus one,}$$

which implies that

$$\inf_{|z|=1} \mathrm{Re}\left[\frac{G(z)}{z-1}\right] = \inf_{\theta\in[0,2\pi)} \mathrm{Re}\left[\frac{G(\mathrm{e}^{\mathrm{i}\theta})}{\mathrm{e}^{\mathrm{i}\theta}-1}\right] \geq G'(1) - \frac{G(1)}{2}. \tag{A.5}$$

From Coughlan and Logemann (2009) we have that γ satisfies $-\infty < \gamma \leq \frac{-G(1)}{2} < 0$ as $G(1) > 0$, and so

$$0 > \gamma \geq \inf_{\theta\in[0,2\pi)} \mathrm{Re}\left[\frac{G(\mathrm{e}^{\mathrm{i}\theta})}{\mathrm{e}^{\mathrm{i}\theta}-1}\right] \geq G'(1) - \frac{G(1)}{2}, \tag{A.6}$$

where we have used the estimate (A.5). It is clear from $\gamma \leq \frac{-G(1)}{2}$ and (A.6) that $G'(1) < 0$ and consequently inequality (A.6) is equivalent to

$$0 < -\gamma = |\gamma| \leq -G'(1) + \frac{G(1)}{2} = |G'(1)| + \frac{G(1)}{2} =: \frac{1}{\kappa},$$

which implies (3.24).

• The constants μ_g and ν_g in (3.16) and (3.20) are given by

$$\mu_g := \sum_{j=0}^{\infty} \left| \begin{bmatrix} c^T & 0 \end{bmatrix} \begin{bmatrix} A & b \\ -gc^T & 1 \end{bmatrix}^j \begin{bmatrix} 0 \\ g \end{bmatrix} \right| \quad \text{and} \quad \nu_g := \sum_{j=0}^{\infty} \left| \begin{bmatrix} c^T & 0 \end{bmatrix} \begin{bmatrix} A & b \\ -gc^T & 1 \end{bmatrix}^j \begin{bmatrix} b \\ 0 \end{bmatrix} \right|,$$

respectively, which are both finite since by assumption $g > 0$ is such that $A_g = \left[\begin{smallmatrix} A & b \\ -gc^T & 1 \end{smallmatrix}\right]$ has $\rho(A_g) < 1$.

• We now derive the inequality (3.29). For complex z with modulus greater than or equal to one the transfer function G given by (3.11) of the linear system (3.5) can be written as

$$G(z) = \sum_{j=0}^{\infty} g_j z^{-j}, \quad \text{where} \quad g_j = \begin{cases} 0, & j = 0, \\ c^T A^{j-1} b, & j \geq 1\,. \end{cases}$$

We define $z \mapsto \tilde{G}(z) := zG(z)$ and introduce the constant

$$\tilde{\gamma} := \sup_{q\geq 0} \left\{ \inf_{\theta\in[0,2\pi)} \mathrm{Re}\left[\left(\frac{q}{\mathrm{e}^{i\theta}} + \frac{1}{\mathrm{e}^{i\theta}-1}\right)\tilde{G}(\mathrm{e}^{i\theta})\right]\right\}.$$

We know that $-\infty < \tilde{\gamma} \leq -\frac{\tilde{G}(1)}{2} = -\frac{G(1)}{2}$. By inspection of the definition of $\tilde{G}$, the constant $\tilde{\gamma}$, and γ_0 in (3.29) we see that

$$\tilde{\gamma} = \gamma_0, \tag{A.7}$$

$$\tilde{G}'(z) = G(z) + zG'(z) \quad \text{and so} \quad \tilde{G}'(1) = G(1) + G'(1)\,. \tag{A.8}$$

We note from (A.8) that

$$\tilde{G}'(1) = G(1) + G'(1) = \sum_{j=1}^{\infty} g_j z^{-j} - \sum_{j=1}^{\infty} j g_j z^{-j} = \sum_{j=1}^{\infty} (1-j) g_j z^{-j} \leq 0\,, \tag{A.9}$$

and consequently we can apply the estimate (3.24) to $\tilde{G}$ to yield that

$$\frac{2}{\tilde{G}(1) + 2|\tilde{G}'(1)|} \leq \frac{1}{|\tilde{\gamma}|}\,. \tag{A.10}$$

In light of (A.7), (A.8) and the following definition of κ_0, (A.10) implies that

$$\kappa_0 := \frac{2}{G(1) + 2|G(1) + G'(1)|} = \frac{2}{\tilde{G}(1) + 2|\tilde{G}'(1)|} \le \frac{1}{|\tilde{\gamma}|} = \frac{1}{|\gamma_0|},$$

as required. Finally, as $G(1) > 0$, it is clear from (A.9) that $G'(1) \le \tilde{G}'(1) \le 0$ and thus

$$|G(1) + G'(1)| = |\tilde{G}'(1)| < |G'(1)|. \tag{A.11}$$

From inequality (A.11) we deduce that

$$\kappa = \frac{2}{G(1) + 2|G'(1)|} < \frac{2}{G(1) + 2|G(1) + G'(1)|} = \kappa_0.$$

A.2 Proof of Theorem 3.4

Let (x, u) denote the solution of

$$\left.\begin{array}{ll} x(t+1) = Ax(t) + bu(t), & x(0) = x^0, \\ u(t+1) = u(t) + g(r - (1 + \varepsilon(t))c^T x(t)), & u(0) = u^0, \end{array}\right\} \quad t = 0, 1, 2, \ldots, \tag{A.12}$$

the integral control system (3.10) with proportional observation errors $\varepsilon(t)$. When ε is a sequence of random variable then so are x and u. We let

$$x_* = (I - A)^{-1} b \frac{r}{G(1)}, \quad u_* = \frac{r}{G(1)},$$

which are equilibria of (3.10) as in (3.12). For notational convenience we define the random variable

$$z(t) := \begin{bmatrix} x(t) - x_* \\ u(t) - u_* \end{bmatrix}, \quad t = 0, 1, 2, \ldots, \tag{A.13}$$

a vector with $n + 1$ components. A short calculation using (3.12) and (A.12) demonstrates that $z(t)$ has dynamics given by

$$z(t+1) = \left[\begin{bmatrix} A & b \\ -gc^T & 1 \end{bmatrix} - \begin{bmatrix} 0 \\ 1 \end{bmatrix} g\varepsilon(t) \begin{bmatrix} c^T & 0 \end{bmatrix} \right] z(t) - \begin{bmatrix} 0 \\ 1 \end{bmatrix} gr\varepsilon(t), \quad t = 0, 1, 2, \ldots. \tag{A.14}$$

We introduce the notation

$$A_g := \begin{bmatrix} A & b \\ -gc^T & 1 \end{bmatrix}, \quad D := \begin{bmatrix} 0_{n\times 1} \\ 1 \end{bmatrix}, \quad E := \begin{bmatrix} c^T & 0 \end{bmatrix},$$

where recall that $0_{n\times 1}$ is a column vector of n zeros. With this notation (A.14) can be more concisely expressed as

$$z(t+1) = [A_g - g\varepsilon(t)DE]\, z(t) - Dgr\varepsilon(t), \quad t = 0, 1, 2, \ldots. \tag{A.15}$$

Letting $\overline{z(t)} = \mathbb{E}(z(t))$ denote the expectation of $z(t)$, we take expectations in (A.15) to yield that

$$\overline{z(t+1)} = A_g \overline{z(t)}, \quad t = 0, 1, 2, \ldots, \tag{A.16}$$

where we have used the facts that expectation is linear, $\overline{\varepsilon(t)} = 0$ and that $\varepsilon(t)$ and $z(t)$ are independent. We are assuming that the gain parameter $g > 0$ is such that $\rho(A_g) < 1$, and hence from (A.16) we conclude that

$$\lim_{t\to\infty} \overline{z(t)} = 0, \quad \text{and thus} \quad \lim_{t\to\infty} \overline{y(t)} = \lim_{t\to\infty} \begin{bmatrix} c^T & 0 \end{bmatrix} \overline{z(t)} + r = r,$$

establishing claim (1). We now consider the covariance

$$\begin{aligned} \operatorname{cov}(z(t), z(t)) &= \mathbb{E}\left((z(t) - \overline{z(t)})(z(t) - \overline{z(t)})^T\right) = \mathbb{E}(z(t)z^T(t)) - \overline{z(t)} \cdot \overline{z^T(t)} \\ &=: C(t) - \overline{z(t)} \cdot \overline{z^T(t)}, \quad t = 0, 1, 2, \ldots, \end{aligned} \tag{A.17}$$

where $z^T(t) = (z(t))^T$. We focus on the quantity $C(t)$, which (appealing to (A.15)) has dynamics

$$
\begin{aligned}
C(t+1) &= \mathbb{E}(z(t+1)z^T(t+1)) \\
&= \mathbb{E}\left([[A_g - g\varepsilon(t)DE]z(t) - Dgr\varepsilon(t)]\,[[A_g - g\varepsilon(t)DE]z(t) - Dgr\varepsilon(t)]^T\right) \\
&= \mathbb{E}(A_g z(t)(A_g z(t))^T) + \underbrace{\mathbb{E}(A_g z(t)z^T(t)(-g\varepsilon(t))(DE)^T) + \mathbb{E}((A_g z(t)z^T(t)(-g\varepsilon(t))(DE)^T)^T)}_{=0} \\
&\quad + \underbrace{\mathbb{E}(A_g z(t)\varepsilon(t)D^T gr) + \mathbb{E}((A_g z(t)\varepsilon(t)D^T gr)^T)}_{=0} + g^2\sigma^2\mathbb{E}(DEz(t)z^T(t)(DE)^T) \\
&\quad + g^2r^2\sigma^2 DD^T + \mathbb{E}(D(-g\varepsilon(t))Ez(t)\varepsilon(t)(-D^T gr)) + \mathbb{E}((D(-g\varepsilon(t))Ez(t)\varepsilon(t)(-D^T gr))^T),
\end{aligned} \tag{A.18}
$$

for $t = 0, 1, 2, \ldots$. Equation (A.18) simplifies to

$$
\begin{aligned}
C(t+1) &= A_g C(t) A_g^T + g^2\sigma^2(DE)C(t)(DE)^T + g^2\sigma^2 r^2 DD^T + rg^2\sigma^2 DE\overline{z(t)}D^T \\
&\quad + rg^2\sigma^2(DE)^T D\overline{z^T(t)}, \quad t = 0, 1, 2, \ldots.
\end{aligned} \tag{A.19}
$$

Define $A_1 := A_g$, $A_2 := g\sigma DE$ and write

$$
c(t) := \operatorname{vec} C(t), \quad p(t) := \operatorname{vec}\left(g^2\sigma^2 r^2 DD^T + rg^2\sigma^2 DE\overline{z(t)}D^T + rg^2\sigma^2(DE)^T D\overline{z^T(t)}\right), \tag{A.20}
$$

where if x_i are the columns of the $n \times n$ matrix $X = [x_1, x_2, \ldots, x_n]$ then

$$
\operatorname{vec} X := \begin{bmatrix} x_1^T & x_2^T & \ldots & x_n^T \end{bmatrix}^T \in \mathbb{R}^{n^2}.
$$

Arguing now as in Ran and Reurings (2002), the matrix difference equation (A.19) can be written as the $(n+1)^2 \times (n+1)^2$ linear system

$$
c(t+1) = \left(\sum_{i=1}^{2} A_i \otimes A_i\right) c(t) + p(t), \quad t = 0, 1, 2, \ldots, \tag{A.21}
$$

where $\otimes$ denotes the Kronecker product. Using the fact that $\overline{z(t)} \to 0$ as $t \to \infty$ it follows from (A.20) that

$$
\lim_{t\to\infty} p(t) = \operatorname{vec}(g^2\sigma^2 r^2 DD^T) =: p_\infty.
$$

Consequently, if

$$
\rho\left(\sum_{i=1}^{2} A_i \otimes A_i\right) = \rho(A_1 \otimes A_1 + A_2 \otimes A_2) < 1, \tag{A.22}
$$

then for any initial condition $c(0)$ the solution c of (A.21) converges to a finite limit c_∞ satisfying

$$
c_\infty = \left(\sum_{i=1}^{2} A_i \otimes A_i\right) c_\infty + p_\infty. \tag{A.23}
$$

Assuming that (A.22) holds, defining C_∞ as the matrix such that

$$
c_\infty = \operatorname{vec} C_\infty,
$$

we have from (A.23) that C_∞ must satisfy

$$
C_\infty = A_g C_\infty A_g^T + g^2\sigma^2(DE)C_\infty(DE)^T + g^2\sigma^2 r^2 DD^T.
$$

Furthermore, as $C(t)$ converges to C_∞ the iterative scheme (A.19) provides a method for approximating C_∞.

It remains to find a characterisation of the stability condition (A.22). Recalling that for square matrices X, Y

$$\sigma(X \otimes Y) = \{\lambda\mu \,:\, \lambda \in \sigma(X), \mu \in \sigma(Y)\},$$

we have that

$$\rho(A_1 \otimes A_1) = \rho(A_g \otimes A_g) = \rho(A_g)^2 < 1,$$

and thus we can view $A_1 \otimes A_1 + A_2 \otimes A_2$ as a structured perturbation of $A_1 \otimes A_1$. Therefore we can characterise the condition (A.22) by appealing to stability radius arguments (Hinrichsen and Pritchard, 1986a,b). A calculation shows that $A_2 \otimes A_2$ is a rank one perturbation, namely

$$A_2 \otimes A_2 = g^2\sigma^2 \begin{bmatrix} 0 & 0 \\ c^T & 0 \end{bmatrix} \otimes \begin{bmatrix} 0 & 0 \\ c^T & 0 \end{bmatrix} = g^2\sigma^2 \begin{bmatrix} 0_{(n^2+2n)\times 1} \\ 1 \end{bmatrix} \begin{bmatrix} (c^T \quad 0) \otimes (c^T \quad 0) \end{bmatrix} =: g^2\sigma^2 \tilde{D}\tilde{E}.$$

Therefore, condition (A.22) is satisfied if and only if

$$\sigma^2 g^2 < \frac{1}{\max\limits_{|z|=1} |\tilde{E}(zI - A_g \otimes A_g)^{-1}\tilde{D}|},$$

which is equivalent to the condition (3.18). We can now take the limit as $t \to \infty$ in (A.17) and use that $z(t)$ converges to zero to deduce that

$$\lim_{t\to\infty} \operatorname{cov}\,(z(t), z(t)) = \lim_{t\to\infty} C(t) = C_\infty. \tag{A.24}$$

The variance of the output satisfies

$$\begin{aligned} \operatorname{var} y(t) &= \operatorname{var}\,(y(t) - r) = \operatorname{var}\left(\begin{bmatrix} c^T & 0 \end{bmatrix} z(t)\right) = \operatorname{cov}\left(\begin{bmatrix} c^T & 0 \end{bmatrix} z(t), \begin{bmatrix} c^T & 0 \end{bmatrix} z(t)\right) \\ &= \begin{bmatrix} c^T & 0 \end{bmatrix} \operatorname{cov}\,(z(t), z(t)) \begin{bmatrix} c \\ 0 \end{bmatrix}, \quad t = 0, 1, 2, \ldots. \end{aligned} \tag{A.25}$$

Therefore taking limits in (A.25) and invoking (A.24) we have that

$$\lim_{t\to\infty} \operatorname{var} y(t) = \begin{bmatrix} c^T & 0 \end{bmatrix} C_\infty \begin{bmatrix} c \\ 0 \end{bmatrix} < \infty,$$

proving claim (2).

A.3 More general input nonlinearities

We comment further on Remarks 3.9 and 3.12. Theorem 3.6 applies when ϕ in (3.21) is replaced by any function $\phi : \mathbb{R} \to \mathbb{R}$ that satisfies a so–called Lipschitz condition, namely

(A3) there exists $l > 0$ such that $0 \le \phi(v) - \phi(w) \le l(v - w)$ for all $v \ge w$.

The constant l in assumption **(A3)** is called the Lipschitz constant of ϕ and, for example, the function ϕ in (3.21) satisfies **(A3)** with $l = 1$.

For a function $\phi : \mathbb{R} \to \mathbb{R}$ and a set $X \subseteq \mathbb{R}$ we let $\operatorname{im}\phi$ and $\phi^{-1}(X)$ denote the image of ϕ and preimage of X of under the function ϕ respectively. In this more general setting, Theorem 3.6 can be restated as: Assume that (3.22) satisfies **(A1)**–**(A3)**. Then, for every $r \in \mathbb{R}$ such that $r/G(1) \in \operatorname{im}\phi$, every $g \in (0, 1/|\gamma l|)$ and all initial conditions $(x^0, u^0) \in \mathbb{R}^n \times \mathbb{R}$, statements (1), (2) and (3) hold. Moreover, if additionally $\phi^{-1}(r/G(1))$ is a singleton then (x^r, u^r) is a globally asymptotically stable equilibrium of (3.22).

The adaptive integral control result, Theorem 3.11, can be restated as: Assume that (3.26) satisfies assumptions **(A1)**–**(A3)**. Then, for every $r \in \mathbb{R}$ such that $r/G(1) \in \operatorname{im}\phi$, and all initial conditions $(x^0, u^0, h^0) \in \mathbb{R}^n \times \mathbb{R} \times (0, \infty)$,

(1) $\lim_{t\to\infty} u(t) = \dfrac{r}{G(1)}$,

(2) $\lim_{t\to\infty} x(t) = x^r := (I - A)^{-1} b \dfrac{r}{G(1)}$,

(3) $\lim_{t\to\infty} y(t) = \lim_{t\to\infty} c^T x(t) = r$.

Moreover, if $\phi^{-1}(r/G(1))$ is a singleton, then

(4) the non-increasing gain $k(t) = 1/h(t)$ converges to a positive limit as $t \to \infty$,

(5) $\lim_{t\to\infty} w(t) = w^r$, where $\phi(w^r) = \dfrac{r}{G(1)}$.

A.4 Proof of Theorem 3.14

By assumption $k > 0$ is chosen so that $A - kbc^T$ is componentwise nonnegative. Since A, b and c^T are also componentwise nonnegative we clearly have that $A \geq A - kbc^T$ (the inequality is understood componentwise) and so Berman and Plemmons (1994, p. 27) implies that

$$0 \leq \rho(A - kbc^T) \leq \rho(A) < 1.$$

We deduce that assumption **(A1)** holds for $A - kbc^T$. Moreover, one can show that the transfer function of $(A - kbc^T, b, c^T)$ is

$$z \mapsto G_k(z) = \frac{G(z)}{1 + kG(z)}, \quad \text{so that} \quad G_k(1) = \frac{G(1)}{1 + kG(1)} > 0,$$

implying that assumption **(A2)** applies to $(A - kbc^T, b, c^T)$. Therefore Theorem 3.1 now applies to the feedback system (3.30), that is the original integral control system (3.10) with A replaced by $A - kbc^T$. It is straightforward to demonstrate that the equilibria (x^*, u^*) of (3.30) are the same as those of (3.10).

A.5 IPM example

Following Briggs et al. (2010) we take $\Omega = [\mathrm{e}^{-0.5}, \mathrm{e}^{3.5}]$, so that $\alpha = \mathrm{e}^{-0.5} \sim 0.6$ and $\beta = \mathrm{e}^{3.5} \sim 33$. The kernel k is divided into

$$k(y, x) = p(y, x) + f(y, x),$$

where p denotes the survival component and f denotes the reproductive component. These have respective decompositions

$$p(y, x) = s(x)(1 - f_p(x))g(y, x), \quad \text{and} \quad \mathrm{f}(y, x) = P_e J(y) s(x) f_p(x) S(x).$$

The functions s, f_p, g, J, S and constant P_e are as in (Briggs et al., 2010, Table 1), where a biological interpretation is also provided. For our simulations we have altered s, S and P_e to

$$s(x) = 0.7 \frac{\mathrm{e}^{0.85x - 0.62}}{1 + \mathrm{e}^{0.85x - 0.62}}, \quad S(x) = \mathrm{e}^{1.85x + 0.37}, \quad P_e = 0.05.$$

We have made these alterations so that the population is declining, and we can apply our results.

Finite element approximations are one method of reducing the infinite–dimensional IPM to a finite–dimensional difference equation by discretising the spatial domain. That is, the function space $L^1(\Omega)$ is approximated by an indexed sequence of finite–dimensional subspaces which get 'closer' to $L^1(\Omega)$ as the index N increases. In what follows we give a very brief description of how finite elements is used to derive an approximation of the IPM and refer the reader to the texts by Johnson (1987) or Brenner and Scott (1994) for a thorough treatment.

For an integer N, the interval $[\alpha, \beta]$ is partitioned into N subintervals with $N+1$ equally spaced endpoints s_i defined by

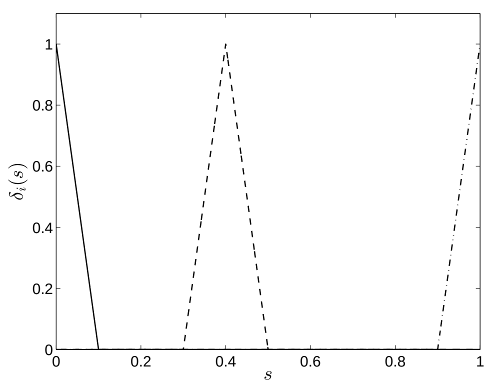
$$s_i = \alpha + \frac{(i-1)(\beta-\alpha)}{N}, \quad 1 \le i \le N+1.$$

In particular $s_1 = \alpha$ and $s_{N+1} = \beta$. The $N+1$ 'hat' or 'tent' functions δ_i are defined by

$$\delta_i(s) = \begin{cases} \dfrac{s - s_{i-1}}{s_i - s_{i-1}} & s \in [s_{i-1}, s_i], \\ \dfrac{s_{i+1} - s}{s_{i+1} - s_i} & s \in [s_i, s_{i+1}], \\ 0 & \text{otherwise}, \end{cases} \quad 1 \le i \le N+1, \tag{A.26}$$

where $s_0 = s_1 = \alpha$ and $s_{N+2} = s_{N+1} = \beta$. The hat functions are more readily understood visually, and some examples are plotted in Figure A.1.

Figure A.1: Three sample hat functions defined by (A.26) with $\alpha = 0$, $\beta = 1$ and $N = 10$. The functions δ_1, δ_5 and δ_{11} are plotted in solid, dashed and dashed–dotted lines respectively.



Loosely speaking, the finite element method assumes that functions in $L^1(\Omega)$ are well approximated by a linear combination of finitely many of the δ_i functions. And so, supposing that n is a solution of the IPM (3.5), using (3.32), (3.34) and (3.35), with input u and output y then for any continuous function v the following equation is satisfied

$$\int_{\xi\in\Omega} v(\xi)\left[n(\xi,t+1) - (An)(\xi,t) - b(\xi)u(t)\right]\, d\xi = 0, \quad t = 0,1,2,\ldots. \tag{A.27}$$

We assume that v and n can be written as a linear combination of the δ_i, that is, as

$$v(t,\xi) = \sum_{i=1}^{N+1} v_i(t)\delta_i(\xi), \quad n(t,\xi) = \sum_{j=1}^{N+1} n_j(t)\delta_j(\xi), \tag{A.28}$$

for some coefficients v_i and n_j. Substituting (A.28) into (A.27) and simplifying gives the following matrix equation

$$M\mathtt{n}(t+1) = D\mathtt{n}(t) + Ju(t), \quad t = 0,1,2,\ldots, \tag{A.29}$$

where $\mathtt{n}(t) = \begin{bmatrix} n_1(t) & \ldots & n_{N+1}(t)\end{bmatrix}^T$ and the matrices M, D and vector J have components given by

$$\left.\begin{aligned} M_{ij} &= \int_{\xi\in\Omega} \delta_i(\xi)\delta_j(\xi)\, d\xi, & D_{ij} &= \int_{\xi\in\Omega} \delta_i(\xi)\int_{s\in\Omega} k(\xi,s)\delta_j(s)\, ds d\xi, \\ J_i &= \begin{bmatrix} J_1 & \ldots & J_{N+1}\end{bmatrix}^T, & J_i &= \int_{\xi\in\Omega} \delta_i(\xi)b(\xi)\, d\xi, \end{aligned}\right\} \quad 1 \le i,j \le N+1.$$

It is straightforward to see that the matrix M is invertible; if $q \in \mathbb{C}^{N+1}$ has i^{th} component q_i then we see that

$$\overline{q}^T M q = \sum_{i,j=1}^{N+1} \overline{q_i} M_{ij} q_j = \int_{\xi\in\Omega} \left\| \sum_{i=1}^{N+1} q_i \delta_i(\xi) \right\|^2 \, d\xi \geq 0\,. \tag{A.30}$$

Furthermore, if $\overline{q}^T M q = 0$ then as $\xi \mapsto \sum_{i=1}^{N+1} q_i \delta_i(\xi)$ is continuous it follows from (A.30) that

$$\sum_{i=1}^{N+1} q_i \delta_i(\xi) = 0, \quad \forall\, \xi \in \Omega \quad \Rightarrow \quad q_i = 0, \quad \forall\, i \in \{1, 2, \dots, N+1\}\,,$$

and thus $q = 0$, proving that M is invertible.

When the output is of the form

$$y(t) = \int_{\xi_1}^{\xi_2} n(s,t)\, ds, \quad t = 0, 1, 2, \dots\,, \tag{A.31}$$

where $\xi_1 < \xi_2$ denote the range of stage–classes observed, then substituting (A.28) into equation (A.31) gives $y(t) = F\mathtt{n}(t)$, where the row vector $F = \begin{bmatrix} F_1 & \dots & F_{N+1} \end{bmatrix}$ has components

$$F_i = \int_{\xi_1}^{\xi_2} \delta_i(s)\, ds, \quad 1 \leq i \leq N+1.$$

Therefore, we have the following system with $N+1$ states

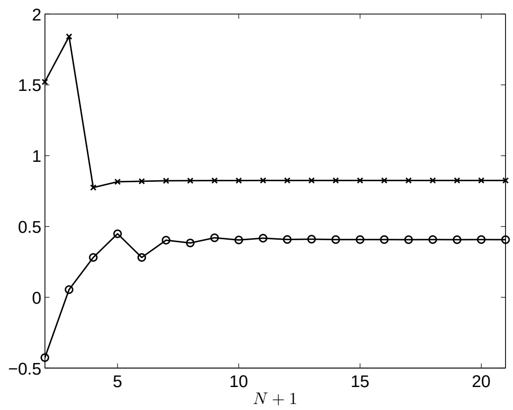
$$\left.\begin{aligned} \mathtt{n}(t+1) &= M^{-1} D \mathtt{n}(t) + M^{-1} J u(t), \\ y(t) &= F\mathtt{n}(t), \end{aligned}\right\} \quad t = 0, 1, 2, \dots, \tag{A.32}$$

which is an approximation of the IPM (3.5) and can be readily implemented. The matrix M and vector F can be found analytically, whilst D and J generally need to be computed numerically. This can be achieved using quadrature, or for example the Matlab functions `integral` and `integral2`. In principle, larger N gives rise to a closer approximation, but clearly adds complexity to simulations. We denote by G_N the transfer function of (A.32) so that the steady–state gain of (A.32) is

$$G_N(1) = F(I - M^{-1}D)^{-1} M^{-1} J,$$

(whenever $\rho(M^{-1}D) < 1$). For our example we worked on the log of the interval $[\alpha, \beta]$, as this gave better results. As such the above goes through with $s_1 = -0.5$, $s_{N+1} = 3.5$. Figure A.2 plots both the spectral radius of $M^{-1}D$ and the steady state gain $G_N(1)$ for increasing N. The figure suggests that both converge for $N \geq 10$ and thus we choose $N = 12$ for the simulations in Figure 3.11. Furthermore, this suggests that the model in Example 3.18 satisfies both assumptions **(A1′)** and **(A2′)**.

Figure A.2: Spectral radius in solid–crossed and steady–state gain in solid–circled of the finite element approximations (A.32) of the IPM model of platte thistle of Example 3.18.



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