Manuscript submitted to
AIMS' Journals
Volume **X**, Number **0X**, XX **200X**

doi:10.3934/xx.xx.xx.xx

pp. **X–XX**

DYNAMIC OBSERVERS FOR UNKNOWN POPULATIONS

Chris Guiver*

Department of Mathematical Sciences
University of Bath
Bath, BA2 7AY, UK

Nathan Poppelreiter

Boston Fusion Corporation
Lexington, MA 02421

Richard Rebarber

Department of Mathematics
University of Nebraska-Lincoln
Lincoln, NE 68588-0130

Brigitte Tenhumberg

Department of Biological Sciences and Mathematics
University of Nebraska-Lincoln
Lincoln, NE 68588-0130

Stuart Townley

Environment and Sustainability Institute
College of Engineering, Mathematics and Physical Sciences
University of Exeter, Penryn campus
Penryn, TR10 9FE, UK

(Communicated by the associate editor name)

Abstract. Dynamic observers are considered in the context of structured-population modeling and management. Roughly, observers combine a known measured variable of some process with a model of that process to asymptotically reconstruct the unknown state variable of the model. We investigate the potential use of observers for reconstructing population distributions described by density-independent (linear) models and a class of density-dependent (nonlinear) models. In both the density-dependent and -independent cases, we show, in several ecologically reasonable circumstances, that there is a natural, optimal construction of these observers. Further, we describe the robustness these observers exhibit with respect to disturbances and uncertainty in measurement.

Date: 31st May 2020.

2010 *Mathematics Subject Classification.* Primary: 39A30, 92D40, 93B51, 93B52, 93C05, 93C10, 93D09.

Key words and phrases. adaptive management, dynamic observer, input-to-state stability, Lur'e system, population ecology, positive system.

* Corresponding author.

1. **Introduction.**

How can we predict a stage-structured population from merely knowledge of repeated measurements of part of that population, for instance just a single stage-class or life-stage? We might annually census nesting turtles and the eggs they lay, but would like to obtain knowledge of the entire population structure, including pelagic life stages which spend a considerable portion of the year in oceans, where measuring is expensive, laborious, and ineffective. Likewise, the seeds of numerous plants species spend a year or more underground before germinating, while other plant species may retreat underground in a dormant state. While knowing the entire plant population distribution might be useful, for example, for management purposes, such life stages are inherently difficult to measure.

We propose that the above ecological problem can be addressed by appealing to dynamic observers, a core component of mathematical control theory [24, 59]. Observers have numerous applications in science and engineering. A selection of examples includes, but is by no means restricted to, bone imaging [62], wastewater treatment [33], chemical reactors [60], secure communications [41] and, recently, applications such as state-of-charge of batteries [39]. The idea of dynamic observers is to combine measurements with a good model to build an estimate of the unknown, but desired, population distribution $x(t)$. Techniques related to the combination of models and measurements also go by the term *data assimilation* in, for example, meteorology [49]. In this work, t is assumed to be a discrete time variable, a ubiquitous assumption in ecological modeling. Moreover, x is assumed to be stratified into a discrete number of stage-classes (such as insect instars) or age-classes. A model for x is assumed, and some measured portion of x is known, denoted y. As we shall discuss later, the measurement is likely to be inaccurate, and so subject to noise.

The principle of a dynamic observer in this context is illustrated in Figure 1.1. The left box demonstrates a life-cycle graph of the population of interest (see, for example, [38, Section 3.7]), which for the purposes of this example has four stages (the numbered nodes) with transitions between these stages (the directed lines) over one time-step. The life-cycle graph becomes a model by assuming some functional forms for the transitions, which models the life history of individuals, but for simplicity the functional forms are not indicated in Figure 1.1. Suppose that at each time-step the abundance of the second stage-class is measured, and denoted by $y(t)$. The observer, the right box, is a virtual copy of the life-cycle graph. The model output, the population structure at the next time-step, is computed by using virtual information for stages one, three and four, and the measured variable $y(t)$. In other words, the virtual model output is updated and augmented with real measured data. The state estimation problem is to formulate assumptions on the model and the measured variable which ensure that the observer synchronizes its *known* predicted population with the *unknown* population, or at least, the unknown population predicted by the model. Such a process provides a dynamic estimate of the whole population which improves over time.

An important ingredient in the present setting is a good population model. Arguably the simplest class of discrete-time, deterministic models for stage-structured populations are linear models, that is

$$x(t+1) = Ax(t) + v(t), \quad x(0) = x_0, \quad t = 0, 1, 2, \ldots . \tag{1.1}$$

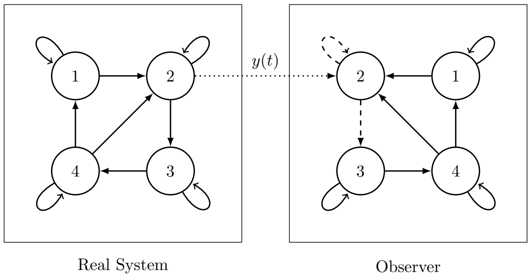


Figure 1.1. Illustration of a dynamic observer. The dashed lines in the right-hand figure at computed using the measured variable $y(t)$.

In an ecological setting, (1.1) is often called a (matrix) population projection model (PPM); see, for example [6] or [11]. Here the vector $x(t)$ denotes the structured population at time-step t and v denotes a disturbance signal which, depending on the setting, describes otherwise unmodelled dynamics, migration, or other external disturbances. For simplicity we use the term *forcing* to describe v abstractly. The matrix A in the PPM (1.1) describes the life history parameters of the population such as survival, growth, stage movement, and fecundity. Without knowledge of $x(t_0)$ for some $t_0 = 0, 1, 2, \ldots$, and in the presence of forcing $v(t)$, we cannot use (1.1) to compute $x(t)$ for $t \geq t_0$. Thus, our underlying and crucial assumptions are that x_0 in (1.1) is *unknown* and v is in general non-zero.

The linear model (1.1) may predict unbounded exponential growth, which is clearly not biologically possible. A more reasonable assumption is that survival, growth, or recruitment are dependent on the size of the population, owing to the effects of intraspecific competition at higher population abundance. Such a system is referred to as *density-dependent*, as opposed to the *density-independent* system in (1.1), and incorporates nonlinear terms. One class of such examples takes the form

$$x(t+1) = Ax(t) + bf(k^T x(t)) + v(t), \quad x(0) = x_0, \quad t = 0, 1, 2, \ldots, \tag{1.2}$$

where A, b and k are appropriately sized matrices/vectors and f is a (nonlinear) nonnegative-valued function with $f(0) = 0$. Again the vector $x(t)$ denotes the structured population at time-step t and v is a forcing term with the same interpretation as that in (1.1). Evidently, (1.2) comprises a linear (density-independent) component, and a non-linear (density-dependent) component. The biological interpretation of (1.2) depends on the context, for instance the matrix A may include survival and growth between stage-classes whilst f represents density-dependent recruitment into the population. In this setting, $k^T x$ is a weighted combination of reproductive stage-classes of x, which recruit $f(k^T x)$ new individuals into the population, distributed over one time-step according to b. For more biological background the reader is referred to [14, 15], for example. In mathematical control theory, models of the form (1.2) are often called Lur'e systems after the Soviet scientist A. I. Lur'e who made early contributions to the study of stability properties of continous-time versions of these systems in the 1940s. Although originally studied in the context of engineering problems, Lur'e systems arise naturally in modeling populations with density dependent fecundity; for instance, this can be done for certain fish species [46, p. 316–323]. Much attention has recently been devoted to the study of the stability properties of Lur'e systems in a biological context; including, for example [14, 16, 22, 55, 64]. Part of the appeal and uptake of models of the form (1.2) is that they are amenable to analysis, yet also permit a wide range of ecologically realistic dynamic behaviour. Indeed, it is possible in certain specific situations, see [64], to present "trichotomies of stability" for the unforced ($v = 0$) model (1.2) explicitly in terms of the model data, which ensure that, under certain assumptions, solutions either converge to the zero equilibrium, or a unique non-zero equilibrium (some *carrying capacity*), or diverge.

Here we present results on observer design and subsequent analysis for both (1.1) and (1.2). The observers proposed are based on so-called Luenberger observers [43, 44], but we exploit the ecological structure and the inherent positivity of the models. The challenges posed by the inclusion of the (potentially persistently non-zero) forcing v in (1.1) or (1.2) and, relatedly, the errors incurred in the measurement y have not yet been mentioned, but both sources of uncertainty are likely to be present in realistic ecological scenarios. To analyse the stability of the observers proposed requires a stability notion which accommodates these features. The concept of input-to-state stability (ISS) from nonlinear control theory is an appropriate framework. Roughly, the ISS concept seeks to generalize to forced nonlinear control systems the familiar estimate:

$$\|w(t)\| \leq M\big(\gamma^t \|w(0)\| + \max_{0 \leq \tau \leq t-1} \|v(\tau)\|\big), \quad \forall\, t = 0, 1, 2, \ldots, \tag{1.3}$$

valid for the solution w of the forced linear system (1.1) with exponentially stable (in discrete-time) A. The constants $M \geq 1$ and $\gamma \in (0,1)$ in (1.3) are independent of $w(0)$ and v, and so the bound (1.3) holds uniformly in these terms. Further, observe that the right-hand side of (1.3) has two separate terms for the contribution of $w(0)$ and v to $\|w(t)\|$, and that the former term decays to zero (exponentially in this case) over time.

ISS was introduced in 1989 by Sontag [57] and has developed into a mature stability theory of nonlinear control systems; see, for instance [12, 37, 58]. We note that we will use estimates of the form (1.3) to bound the difference between the known observer state (the predicted population) and the unknown model state — the solutions x of (1.1) or (1.2) themselves need not satisfy (1.3) and, as mentioned earlier, may exhibit other ecologically realistic dynamic behaviour. Our analysis is in the spirit of so-called incremental ISS (see, for example [1]) which seeks to provide estimates of the form (1.3) for the difference between *any* two solutions of (1.2) (not just a solution and the zero equilibrium). Evidently, for linear systems, where the superposition principle holds, the notions of ISS and incremental ISS coincide. We make the important observation that for general nonlinear difference equations, estimates of the form (1.3) *need not* follow from global asymptotic stability results of the unforced version of the difference equation, motivating our use of the ISS framework.

In addition to stability analysis, we show that there are natural candidates for "optimal" observers in a sense we describe. The current work also furthers a line of enquiry of the present authors which, in addition to deriving new control theoretic results, seeks to increase the awareness and uptake of concepts from mathematical systems and control theory in ecological modelling and management where we believe these tools are ideally suited; see, for instance [20, 29, 30].

We comment that underpinning our analysis is the concept of a positive dynamical system, since the state of (1.1) or (1.2) is naturally nonnegative, modeling a necessarily nonnegative quantity. Positive systems are well-studied objects with monographs on the subject including [3, 19, 32], and we design observers which themselves, under ecologically reasonable assumptions on the forcing, also take nonnegative values. We therefore mention that dynamic observers have been proposed as a technique for population estimation in [27], and for positive linear systems in [13, 51, 66]. However, the overlap with the present work is minimal, as each of these papers focusses on different aspects of the linear, continuous-time setting, without forcing. None of the mentioned papers considers observer design for the positive forced Lur'e system (1.1). Dynamic observers for nonlinear control systems is a vast subject in the systems and control literature, and background references include, but are not limited to [2, 18, 25, 40, 67] and the references therein. Again, to the best of our knowledge, the case considered here of positive Lur'e systems in discrete-time subject to forcing has not been considered.

The manuscript is organized as follows. Section 2 contains a problem statement with solutions given in Sections 3 and 4 for the linear and nonlinear settings, respectively. Examples are presented in Section 5, and some further robustness concepts are addressed in Section 6. We make summarizing remarks in Section 7, which also seeks to make connections to other related, and potential future, research areas.

Notation and Terminology

As usual let $\mathbb{N}$, $\mathbb{Z}_+$, $\mathbb{R}$, $\mathbb{R}_+$ and $\mathbb{R}^n$ denote the set of positive and nonnegative integers, the field of real numbers, the set of nonnegative real numbers, and n-dimensional real Euclidean space, respectively. Let $\mathbb{R}^n_+$ denote the set of n-dimensional real vectors with nonnegative entries. We let e_i denote the standard i-th basis vector in $\mathbb{R}^n$. For a vector $v \in \mathbb{R}^n$, with i-th component v_i, we let $|v|$ denote the vector with i-th component $|v_i|$. We let $\|v\|$ denote a (any) monotonic norm of v, that is, $\|v\| = \||v|\|$ see, for example, [35]. Usual Euclidean norms are monotonic, and in ecological applications the Euclidean one-norm is typically the most natural (denoting total abundance).

Let $\mathbb{R}^{m\times n}$ denote the vector space of $m \times n$ real matrices, and let $\mathbb{R}^{m\times n}_+$ denote the set of $m \times n$ real matrices with nonnegative entries, called nonnegative matrices. For $X \in \mathbb{R}^{n\times n}$, let $\rho(X)$ denote the maximum of the moduli of the eigenvalues of X, called the spectral radius of X. For $Y, Z \in \mathbb{R}^{m\times n}$, we let Y^T denote the transpose of Y. The (i, j)-th entry of Y is denoted $Y_{i,j}$ or $(Y)_{i,j}$, and we write $Y \le Z$ or $Y \ge Z$ if $Y_{i,j} \le Z_{i,j}$ for all i, j. We use the same symbols to denote componentwise inequality of vectors. A nonnegative matrix $X \in \mathbb{R}^{n\times n}_+$ is said to be irreducible if, for each i, j with $1 \le i, j \le n$, there is some positive integer $r = r(i, j)$ such that $(X^r)_{i,j} > 0$, or primitive if there is some positive integer r such that $(X^r)_{i,j} > 0$ for all i, j with $1 \le i, j \le n$.

For a sequence $v : \mathbb{Z}_+ \to \mathbb{R}^n$, we let $\pi_t v$ denote the projection onto the first t terms of v, that is, $(\pi_t v)(s) = v(s)$ if $0 \le s \le t$ and $(\pi_t v)(s) = 0$ if $s > t$. Finally, we let $\| \cdot \|_{\ell^p}$ denote the usual ℓ^p norms for sequences for $p \in [1, \infty)$.

2. **Problem statement.** Throughout we let $x(t)$ denote a structured population of interest at the (fixed) discrete time-step $t \in \mathbb{Z}_+$ (for example, a week, month or year). Let n denote the dimension of the vector $x(t)$, so that the population $x(t)$ is

a structured population with n age- or stage-classes. We shall assume in Sections 3 and 4 that x is modelled by (1.1) and (1.2), respectively.

In both cases, we shall assume that at every time-step t, a (possibly noisy) measurement of part of the population is known. We denote these measurements by $y(t)$ which, in the absence of noise, are assumed to be of the form

$$y(t) = Cx(t), \quad t \in \mathbb{Z}_+ .$$

Here $C \in \mathbb{R}_+^{q\times n}$ so that $q \in \mathbb{N}$ denotes the number of distinct measurements of the population taken at each time-step (not to be confused with measuring a given variable(s) repeatedly over time). Since we assume no trivial measurements, we impose throughout that every row of C is nonzero.

Example 2.1. Consider a population with $n = 5$ stage-classes. If $y(t)$ is the abundance of the fourth and fifth stages separately, then

$$y(t) = \begin{pmatrix} x_4(t) \\ x_5(t) \end{pmatrix}, \quad C = \begin{pmatrix} e_4 & e_5 \end{pmatrix}^T = \begin{pmatrix} 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 1 \end{pmatrix} .$$

If $y(t)$ is the *total* abundance of the fourth and fifth stages (that is, we count the fourth and fifth stages but do not distinguish between them), then

$$y = x_4 + x_5, \quad C = e_4^T + e_5^T = \begin{pmatrix} 0 & 0 & 0 & 1 & 1 \end{pmatrix} .$$

Evidently, the form of C depends on the setting. We note that as C maps the state variables x to the measured variables y (which may have different orders of magnitude or units), it may be the case that C has non-integer components. For example, consider a model for spawning fish where the first stage-class is the number of eggs. In most cases it is impracticable to count eggs individually, particularly without disrupting them, and more likely is that the observed size of an egg cluster is a proxy for the number of eggs contained. Thus, measurement of eggs may be in multiples of 500, say. If the first stage class denotes number of eggs, and this is the only measurement, then $C = c^T \in \mathbb{R}_+^{1\times n}$ with $c_1 = 5 \times 10^{-2}$. ◊

To incorporate measurement error, we write

$$y(t) = Cx(t) + d(t), \quad t \in \mathbb{Z}_+ . \tag{2.1}$$

where d in (2.1) is a forcing or noise signal, so that the "true" (but typically unknown) measurement at each time step is $Cx(t)$. Since we are observing a nonnegative quantity $x(t)$, it is reasonable to assume that negative entries in $y(t)$ are caused by noise. Thus, by replacing negative entries by zero, we shall assume throughout that $d(t) \geq -Cx(t)$ for every $t \in \mathbb{Z}_+$, which results in $y(t)$ being nonnegative for every $t \in \mathbb{Z}_+$.

In certain situations it may be appropriate to model the measurement error multiplicatively, capturing errors which are proportional to the current observed quantity, which we can always write as

$$y(t) = (I + \varepsilon(t))Cx(t) = Cx(t) + \varepsilon(t)Cx(t), \quad t \in \mathbb{Z}_+ , \tag{2.2}$$

which is in the form (2.1), and where I denotes the identity matrix. Here $\varepsilon(t)$ is a diagonal matrix with entries in $[-1, \infty)$ for each $t \in \mathbb{Z}_+$, and $\varepsilon(t) = 0$ corresponds to exact measurement. Note that in this case, by our assumptions on $\varepsilon(t)$, it follows that $y(t)$ is nonnegative for every $t \in \mathbb{Z}_+$.

Our goal is to estimate the unknown x by a known quantity, throughout denoted z, which is called the observer state. The two important criteria we wish z to satisfy are:

(O1) The observer state z should be nonnegative.
(O2) For z to estimate x, the error $e = x - z$ should be bounded in terms of the forcing, and converge to zero if the forcing does as well.

The criteria (O1) and (O2) seek to capture desirable qualitative and quantitative properties of the observer, respectively.

3. Linear Systems.

In this section, we assume that x is given by the forced linear PPM model (1.1), recall given by

$$x^+ = Ax + v, \quad x(0) = x_0\,.$$

Here and throughout $x^+(t) = x(t+1)$ for all $t \in \mathbb{Z}_+$, and $x_0 \in \mathbb{R}^n_+$ is the (unknown) initial state. The term v denotes a forcing (also called and interpreted as an input, control action/signal, or disturbance). We shall assume throughout that v is bounded, and that $x(t) \in \mathbb{R}^n_+$ for all $t \in \mathbb{Z}_+$, which is certainly the case if $v(t) \in \mathbb{R}^n_+$ for all $t \in \mathbb{Z}_+$, although $x(t) \in \mathbb{R}^n_+$ for all $t \in \mathbb{Z}_+$ may be satisfied by v which take nonpositive values, see [28].

We assume that $A \in \mathbb{R}^{n\times n}_+$ in (1.1) is irreducible — a natural assumption for ecologically meaningful models [61]. A consequence of the Perron-Frobenius theorem (see, for example, [4, Theorem 1.4, p. 27]) is that $\rho(A)$ is an eigenvalue of A. In practice, we do not know either x_0 or the entries of A precisely, but we assume in this manuscript that A is known, but x_0 is unknown. Recall that for the *unforced* version of (1.1), the cases $\rho(A) < 1$ and $\rho(A) > 1$ correspond to asymptotic population decline to zero and asymptotic population increase without bound, respectively. This latter case is ecologically unrealistic long term, but may be useful for short-term estimation (for example, of an invasive species). However, the observers presented here are asymptotic in that their estimates improve in time, and so the estimates in the short-term may not be suitably accurate.

We propose an observer of the form

$$z^+ = A_0 z + Hy, \quad z(0) = z_0\,, \tag{3.1}$$

where $y(t)$ is given by (2.1), $A_0 := A - HC$, and $H \in \mathbb{R}^{n\times q}$ and $z_0 \in \mathbb{R}^n_+$ are to be determined by the user.

Our key assumption for practicable observer design (3.1) is the following.

(L) There exists a nonzero $H \in \mathbb{R}^{n\times q}_+$ such that $A_0 = A - HC \geq 0$ and $\rho(A_0) < 1$.

We define $\mathcal{S}_\mathrm{l}$ to be set of all nonzero $H \in \mathbb{R}^{n\times q}_+$ such that $A - HC \geq 0$ and $\rho(A - HC) < 1$. Hence, (L) holds if, and only if, $\mathcal{S}_\mathrm{l}$ is nonempty. We shall see in Proposition 3.3 below that $\mathcal{S}_\mathrm{l}$ is nonempty in many ecologically meaningful models.

Combining (1.1), (2.1) and (3.1) gives the linear observed system

$$\left.\begin{aligned} x^+ &= Ax + v, & x(0) &= x_0,\\ z^+ &= A_0 z + Hy, & z(0) &= z_0,\\ y &= Cx + d\,. & & \end{aligned}\right\} \tag{LO}$$

Our main stability result for (LO) is the following.

Proposition 3.1. *Consider the linear model* (1.1)*, with observations* (2.1)*. Assume that* (L) *holds, and let* $H \in \mathcal{S}_1$ *with* $r_0 := \rho(A - HC) \in [0, 1)$ *and* $r \in [1, \infty)$*. Then property* (O1) *holds for* z *given by* (LO)*. Further, there exist positive constants* M *and* M_r *such that, for all* $x_0, z_0 \in \mathbb{R}^n_+$ *and sequences* d *and* v*, the solution* (x, z) *of* (LO) *satisfies*

$$\|x(t) - z(t)\| \leq M\Big(r_0^t \|x_0 - z_0\| + \max_{0 \leq \tau \leq t-1} (\|v(\tau)\| + \|d(\tau)\|)\Big) \quad \forall\, t \in \mathbb{N}\,, \tag{3.2}$$

and

$$\|\pi_t(x - z)\|_{\ell^r} \leq M_r\Big(\|x_0 - z_0\| + \|\pi_{t-1}v\|_{\ell^r} + \|\pi_{t-1}d\|_{\ell^r}\Big) \quad \forall\, t \in \mathbb{N}\,. \tag{3.3}$$

The estimate (3.2) ensures that the observer estimation property (O2) holds.

Proof of Proposition 3.1. Since $H \in \mathcal{S}_1$, it follows that $A_0 \geq 0$. As $z_0 \geq 0$, and $y \geq 0$ by our standing hypothesis, it follows from (3.1) that $z(t) \geq 0$ for all $t \in \mathbb{Z}_+$, hence (O1) holds.

From (LO), we compute that the error $e := x - z$ satisfies

$$e^+ = x^+ - z^+ = Ax + v - A_0 z - Hy = A_0 e + v - Hd\,. \tag{3.4}$$

Since $\rho(A_0) < 1$ by (L), the estimates (3.2) and (3.3) will follow from the expression

$$x(t) - z(t) = A_0^t (x(0) - z(0)) + \sum_{j=0}^{t-1} A_0^{t-1-j}\big(v(j) - Hd(j)\big) \quad \forall\, t \in \mathbb{N}\,, \tag{3.5}$$

for the solution of (3.4). For the latter, let $\mathcal{A}_0$ denote the sequence with t-th value A_0^t. Then (3.5) is the same as

$$(x - z)(t) = \mathcal{A}_0(t)(x(0) - z(0)) + (\mathcal{A}_0 * (v - Hd))(t - 1) \quad \forall\, t \in \mathbb{N}\,,$$

where $*$ denotes discrete convolution. Taking the ℓ^r norm of both sides and using that

$$\|\mathcal{A}_0 * (v - Hd)\|_{\ell^r} \leq \|\mathcal{A}_0\|_{\ell^1} \cdot \|v - Hd\|_{\ell^r} \leq c_r\big(\|v\|_{\ell^r} + \|d\|_{\ell^r}\big)\,,$$

for some $c_r > 0$, gives (3.3). $\square$

We provide some remarks on the above result.

Remark 3.2. (a) The inequality (3.2) is an exponential ISS (input-to-state-stability) estimate, see also the discussion after (1.3). Observe that the first term on the right hand side of (3.1) converges to zero as $t \to \infty$, but the second could be positive if $\|d\|$ and $\|v\|$ have positive lim inf. In this case, we should not expect that $x(t) - z(t) \to 0$ as $t \to \infty$.

(b) The system (LO) is left-shift invariant, meaning if (v, d, x, z) is a solution of (LO) with initial condition (x_0, z_0), then $(v_\tau, d_\tau, x_\tau, z_\tau)$ is also a solution of (LO) with initial condition $(x(\tau), z(\tau))$ for all $\tau \in \mathbb{N}$. Here $x_\tau(t) := x(t+\tau)$ for all $t \in \mathbb{Z}_+$, and similarly for v_τ and so on. A consequence of the left-shift invariance is that if the hypotheses of Proposition 3.1 are satisfied, then the estimate (3.2) may be strengthened to

$$\begin{aligned}\|x(t+s)-z(t+s)\| \leq & M\Big(r_0^t\|x(s)-z(s)\| \\ & + \max_{s\leq\tau\leq s+t-1}(\|v(\tau)\|+\|d(\tau)\|)\Big) \quad \forall\, s,t\in\mathbb{N}\,.\end{aligned}$$

Therefore, if $\max\{\|v(t)\|,\|d(t)\|\}\to 0$ as $t\to\infty$, then $x(t)-z(t)\to 0$ as $t\to\infty$. Similar modifications may be applied to (3.3).

(c) The choice of z_0 may be informed by any partial knowledge of x_0, and making $\|x_0-z_0\|$ smaller provides tighter (that is, better) bounds in (3.2) and (3.3).

(d) In the case that $d=0$ and $v=0$, the error $e=x-z$ dynamics are given by $e(t+1)=A_0e(t)$. Consequently, $e(t)\in\mathbb{R}^n_+$ for all $t\in\mathbb{Z}_+$ if $z_0\leq x_0$, that is, the initial observer state is an underestimate of the initial state. It is always possible to choose $z_0=0$ as a guaranteed underestimate. In this case, z is an underestimate of x, that is, $z(t)\leq x(t)$ for all $t\in\mathbb{Z}_+$.

(e) In the situation that the measurement error is proportional to the true measurement, meaning $d=\varepsilon y$, see (2.2), then the right hand sides of (3.5) may diverge if $\rho(A)>1$ and the infimum of $|\varepsilon(t)|$ is positive. This is a consequence of the shortcomings of linear models which may predict unbounded exponential growth, and is a feature not seen in realistic biological models, such as the nonlinear models considered in Section 4.

(f) Taking $H=0$ is prohibited in (L), as $H=0$ corresponds to the so-called "trivial observer", that is the measurement $y(t)$ does not inform the observer state $z(t)$. When our estimate $z(t)$ fails to be informed by the measurement, it is simply a simulation of the model (1.1) with initial state $z(0)$ and without the forcing v. $\Diamond$

There may be many H in $\mathcal{S}_l$, raising the question of how to (optimally) choose H. Noting that $r_0:=\rho(A-HC)<1$ appears in the upper bound in (3.2), we seek to minimize this quantity. In our next result, we describe the optimal H to minimize r_0 in several ecologically meaningful settings; for examples see Section 5.1. In the next result, $A(j)$ denotes the j-th column of A.

Proposition 3.3. *Given* (LO)*, the following statements hold.*

(a) *There exists $H_*\in\mathbb{R}^{n\times q}_+$ such that $A-H_*C\geq 0$ and*

$$\rho(A-H_*C)\leq\rho(A-HC)\quad\forall\,H\in\mathbb{R}^{n\times q}_+\quad\textit{with}\quad A-HC\geq 0\,. \tag{3.6}$$

(b) *Assume that individual stage-classes are separately observed, that is,*

$$C=\begin{pmatrix}e_{i_1} & \dots & e_{i_q}\end{pmatrix}^T\quad\textit{for}\quad 1\leq i_1<\dots<i_q\leq n\,. \tag{3.7}$$

Then H_1 given by

$$H_1=\begin{pmatrix}A(i_1) & \dots & A(i_q)\end{pmatrix}, \tag{3.8}$$

satisfies $A-H_1C\leq A-HC$ over all $H\in\mathbb{R}^{n\times q}_+$ such that $A-HC\geq 0$, and so (3.6) *holds with $H_*=H_1$. Thus,* (L) *holds if, and only if, $\rho(A-H_1C)<1$.*

(c) *Assume that a collection of stages is observed, that is,*

$$C=\sum_{j=1}^q e_{i_j}^T\quad\textit{for}\quad 1\leq i_1<\dots<i_q\leq n\,. \tag{3.9}$$

Then H_2 given by

$$H_2 = \begin{pmatrix} \min_{k=1,\ldots,q} A_{1,i_k} \\ \vdots \\ \min_{k=1,\ldots,q} A_{n,i_k} \end{pmatrix},$$

satisfies $A - H_2C \leq A - HC$ over all $H \in \mathbb{R}_+^{n\times q}$ such that $A - HC \geq 0$, and so (3.6) *holds with $H_* = H_2$. Thus,* (L) *holds if, and only if, $\rho(A - H_2C) < 1$ and $A - H_2C \neq 0$.*

We comment that there are situations where (L) fails and so statement (a) of Proposition 3.3 holds only with $H = 0$. Evidently, the construction of H is an integral part of the observer design part. However, the choice of $H \in \mathcal{S}_1$ depends on C, capturing which stage-classes are observed. Depending on the context, there may be some choice in the construction of C as well.

Proof of Proposition 3.3: (a) Define the set $\mathcal{T}_1$ of all $H \in \mathbb{R}_+^{n\times q}$ such that $A - HC \geq 0$. It is clear that $\mathcal{T}_1$ is closed and, we claim, bounded. Indeed, let $H \in \mathcal{T}_1$. By the assumption that every row of C is nonzero, for each $j \in \{1, 2, \ldots, q\}$, there exists $k(j) \in \{1, 2, \ldots, n\}$ such that $C_{j,k(j)} > 0$. Consequently, for every $i \in \{1, 2, \ldots, n\}$ and $j \in \{1, 2, \ldots, q\}$

$$A_{i,k(j)} - H_{i,j}C_{j,k(j)} \geq A_{i,k} - \sum_{\ell=1}^{q} H_{i,\ell}C_{\ell,k(j)} = (A - HC)_{i,k(j)} \geq 0\,.$$

We conclude that

$$H_{i,j} \leq \frac{A_{i,k(j)}}{C_{j,k(j)}} \leq \frac{\max_{\ell,r} A_{\ell,r}}{\min_r C_{r,k(r)}} < \infty \quad \forall\, i \in \{1, 2, \ldots, n\},\ \forall\, j \in \{1, 2, \ldots, q\}\,.$$

Therefore, the continuous function $g : \mathcal{T}_1 \to \mathbb{R}_+$ defined by $g(H) = \rho(A - HC)$ attains a minimum in $\mathcal{T}_1$, denoted H_*, which is (3.6).

(b) Note that with H_1 defined as in (3.8), columns i_1 to i_q of $A - H_1C$ are zero. Consequently, there are no $H \in \mathbb{R}_+^{n\times q}$ such that $A - HC \leq A - H_1C$, $A - HC \neq A - H_1C$ *and* $A - HC \geq 0$. It is well-known from, for example [4, Corollary 1.5 (a), p.27], that the inequalities $0 \leq A - H_1C \leq A - HC$ imply that (3.6) holds. To prove the claimed equivalence, suppose that (L) holds. Then there exists $H \in \mathbb{R}_+^{n\times q}$ such that $0 \leq A - HC$ and $\rho(A - HC) < 1$. In light of the first part of statement (b), $\rho(A - H_1C) \leq \rho(A - HC) < 1$, as required. Conversely, if $\rho(A - H_1C) < 1$, then $H_1 \in \mathcal{S}_1$ as A irreducible implies that no column of A is zero, and hence $H_1 \neq 0$ and $0 \leq A - H_1C$. Evidently, $\mathcal{S}_1$ is nonempty and hence (L) holds.

(c) The proof is similar to that of statement (b), and so the details are omitted. □

Remark 3.4. Given (LO), we comment that we should not in general expect a "componentwise minimizing" H_* such that

$$0 \leq A - H_*C \leq A - HC \quad \forall\, H \in \mathbb{R}_+^{n\times q} \quad \text{with} \quad A - HC \geq 0\,,$$

as the pair

$$A = \begin{pmatrix} 1 & 1 & 1 \\ * & * & * \\ * & * & * \end{pmatrix}, \quad C = \begin{pmatrix} 1 & 1 & \frac{1}{2} \\ 0 & \frac{1}{2} & 1 \end{pmatrix},$$

demonstrates. Here $*$ denotes unimportant entries. The matrices

$$H_1 = \begin{pmatrix} 1 & 0 \\ 0 & 0 \\ 0 & 0 \end{pmatrix} \quad \text{and} \quad H_2 = \begin{pmatrix} 0 & 1 \\ 0 & 0 \\ 0 & 0 \end{pmatrix},$$

satisfy

$$A - H_1C = \begin{pmatrix} 0 & 0 & 1 \\ * & * & * \\ * & * & * \end{pmatrix} \quad \text{and} \quad A - H_2C = \begin{pmatrix} 1 & \frac{1}{2} & 0 \\ * & * & * \\ * & * & * \end{pmatrix}.$$

Therefore, for H_* to satisfy $0 \le A - H_*C \le A - H_1C$ and $0 \le A - H_*C \le A - H_2C$, the top row of $A - H_*C$ must equal zero. It is straightforward to see that there is no such H_*. ♢

3.1. **Observability.** We conclude the current section by providing some discussion on the ubiquitous concept from mathematical control theory of observability. Observability pertains to reconstructing x_0, and hence x, from finitely-many measurements y, which ostensibly provides a solution to the problem considered in this paper.

Observability for linear control systems is discussed in most control theory textbooks; see, for example, [24] or [59]. At its heart, the notion appeals to linear algebra as a consequence of the assumed structure in (1.1) and (2.1). The requirement that $d = 0$ and $v = 0$ is crucial to what follows. In this case, we simply note that (1.1) and (2.1) yields a linear system of n equations,

$$y(t) = CA^t x_0, \quad t = 0, ..., n-1,$$

which may be rewritten as

$$Qx_0 := \begin{pmatrix} C \\ CA \\ \vdots \\ CA^{n-1} \end{pmatrix} x_0 = \begin{pmatrix} y(0) \\ y(1) \\ \vdots \\ y(n-1) \end{pmatrix}. \tag{3.10}$$

The matrix $Q \in \mathbb{R}^{mn \times n}$ in (3.10) is known to the user, as is the vector of observations on the right hand side. It follows that (3.10) has a unique solution x_0 if, and only if, Q has full rank (equal to n), in which case (3.10) can be solved for x_0. This calculation underpins the concept of observability.

We are proposing dynamic observers as a solution for the population estimation problem for the following two reasons:

- The above analysis breaks down in the likely situation that v and d are nonzero.
- Generalizing observability as an estimation method for nonlinear systems requires solving a nonlinear version of (3.10). Such a nonlinear system of (possibly many) equations could be much more difficult to solve.

We conclude by highlighting that there is a connection between observability and observers. Specifically, it can be proved that if the pair (A, C) is observable (which is equivalent to $\operatorname{rank} Q = n$), then it is possible to choose H such that the eigenvalues of $A - HC$ are equal to the roots of any real, monic polynomial of degree n. This process is sometimes called pole-placement or eigenvalue-placement in the control engineering jargon. However, pole placement need not respect the nonnegativity constraints we impose for ecological relevance in this paper: $H \geq 0$ such that $A - HC \geq 0$ and $H \neq 0$. Consequently, we do not pursue pole placement as a tool for observer design in this context.

4. **Nonlinear Systems.**

Here we assume that x satisfies

$$x^+ = Ax + bf(k^T x) + v, \quad x(0) = x_0\,, \tag{1.2}$$

where $x_0 \in \mathbb{R}^n_+$; $A \in \mathbb{R}^{n\times n}_+$; $b, k \in \mathbb{R}^n_+$; and $f : \mathbb{R}_+ \to \mathbb{R}_+$ is continuous with $f(0) = 0$. We formulate the assumption on the linear data in (1.2):

(NL1) $\rho(A) < 1$, and $b, k \neq 0$.

The assumptions on A, b and k imposed in (NL1) are not restrictive. A consequence of the assumed nonnegativity is that when $v = 0$, the solution x of (1.2) satisfies the lower bound $x^+ \geq Ax$, and so diverges if $\rho(A) > 1$, which is dynamic behaviour we wish to omit. The case $b = 0$ or $k = 0$ is degenerate and leads to linear models considered in Section 3.

For $(H, j) \in \mathbb{R}^{n\times q}_+ \times \mathbb{R}^q_+$, let $A_0 := A - HC$ and $k_0 := k - C^T j$. We let $\mathcal{S}_{\mathrm{nl}}$ denote the set of all non-zero ordered pairs $(H, j) \in \mathbb{R}^{n\times q}_+ \times \mathbb{R}^q_+$ such that $A_0 \geq 0$ and $k_0 \geq 0$. As with $\mathcal{S}_{\mathrm{l}}$ in Section 3, we shall see in Proposition 4.3 that $\mathcal{S}_{\mathrm{nl}}$ is nonempty for ecologically reasonable $C \in \mathbb{R}^{q\times n}_+$.

We propose an observer of the form

$$z^+ = A_0 z + Hy + bf(k_0^T z + j^T y), \quad z(0) = z_0\,, \tag{4.1}$$

where $(H, j) \in \mathcal{S}_{\mathrm{nl}}$ and $z_0 \in \mathbb{R}^n$ are to be determined by the user.

Combining (1.2), (2.1) and (4.1) gives the nonlinear observed system

$$\left.\begin{aligned} x^+ &= Ax + bf(k^T x) + v, & x(0) &= x_0,\\ z^+ &= A_0 z + Hy + bf(k_0^T z + j^T y), & z(0) &= z_0,\\ y &= Cx + d. \end{aligned}\right\} \tag{NLO}$$

A crucial quantity in the following development is the real-valued function $p : \mathcal{S}_{\mathrm{nl}} \cup \{0\} \to \mathbb{R}_+ \cup \{\infty\}$ defined by

$$p(H, j) = \frac{1}{(k^T - j^T C)\big(I - (A - HC)\big)^{-1} b} \quad \forall\, (H, j) \in \mathcal{S}_{\mathrm{nl}} \cup \{0\}\,,$$

where we use the convention $1/0 = \infty$ for scalar 0. Note that p is well-defined by (NL1), and is nonnegative since the denominator may be written as

$$(k^T - j^T C)\Big(\sum_{j\in\mathbb{N}_0} (A - HC)^j\Big) b \geq 0\,,$$

a sum of nonnegative terms, as $(H, j) \in \mathcal{S}_{\mathrm{nl}} \cup \{0\}$. For notational convenience, we use p_0 to denote the more cumbersome $p(0, 0)$. More commentary on p, including a biological interpretation, is provided in Remark 4.2. From, for example [64, Lemma 3.1], it is known that p_0 is finite if $A + bk^T$ is primitive.

Our main stability result for the observed system (NLO) is the following theorem.

Theorem 4.1. *Consider the nonlinear model* (1.2) *satisfying* (NL1)*, with observations* (2.1)*. Assume that $\mathcal{S}_{\mathrm{nl}}$ is nonempty, and let $(H, j) \in \mathcal{S}_{\mathrm{nl}}$. Then property* (O1) *holds for z given by* (NLO)*. Furthermore, if*

(NL2) *f is μ-Lipschitz, with $\mu < p(H, j)$;*

holds, then with $r_0 := \rho(A_0 + \mu b k_0^T) \in [0, 1)$ and $r \in [1, \infty)$, there exists $M, M_r > 0$ such that, for all $x_0, z_0 \in \mathbb{R}^n_+$ and all sequences d and v, the estimates (3.2) *and* (3.3) *hold for the solution (x, z) of* (NLO)*.*

As with Proposition 3.1, the estimate (3.2) ensures that the observer estimation property (O2) holds.

The conclusions of Theorem 4.1 are still valid if $p(H, j)$ is infinite, provided that f is μ-Lipschitz with some finite Lipschitz constant μ.

Proof of Theorem 4.1. By hypothesis, all the terms involved on the right hand side of (4.1), the dynamic equation for z, are nonnegative. Hence, it follows from (4.1) that $z(t) \geq 0$ for all $t \in \mathbb{Z}_+$, that is, (O1) holds.

Given x_0, z_0, d and v, let (x, z) denote the solution of (NLO), and set $e := x - z$. A routine calculation shows that the error dynamics are given by

$$e^+ = A_0 e + b\big(f(k^T x) - f(k_0^T z + j^T y)\big) + v - Hd, \quad e(0) = x_0 - z_0 \,. \tag{4.2}$$

Taking the vector absolute value in (4.2), using the triangle inequality and the Lipschitz property of f, as well as noting that $|Qw| \leq Q|w|$ for nonnegative matrices Q and all appropriately-sized vectors w, we estimate that

$$\begin{aligned} |e^+| &\leq A_0|e| + b\big|f(k^T x) - f(k_0^T z + j^T y)\big| + |v| + |Hd| \\ &\leq A_0|e| + b\mu\big|k^T x - k_0^T z - j^T y\big| + |v| + |Hd| \\ &= (A_0 + \mu b k_0^T)|e| + \mu b|j^T d| + |v| + |Hd| \\ &= E_0|e| + \eta \,, \end{aligned}$$

where $E_0 := A_0 + \mu b k_0^T$ and $\eta := \mu b|j^T d| + |v| + |Hd|$. Therefore, $|e|$ admits the estimate

$$|e(t)| \leq E_0^t |e(0)| + \sum_{j=0}^{t-1} E_0^{t-1-j} \eta(j) \quad \forall\, t \in \mathbb{N} \,. \tag{4.3}$$

It is well-known from stability radius theory for positive systems (see, for example [35, Theorem 3.4]) that $\mu < p(H, j)$ implies that $\rho(E_0) = \rho(A_0 + \mu b k_0^T) < 1$. Therefore, the bounds (3.2) and (3.3) follow from (4.3), combined with the assumed monotonic norm property $\big\||w|\big\| = \|w\|$. ☐

We provide some commentary on the above result, noting that items (a)–(c) of Remark 3.2 are relevant in the nonlinear setting as well.

Remark 4.2. (a) Stability properties of (1.2) have been considered in the forced case in [20], which builds on the earlier work [64] where the unforced version ($v = 0$) of (1.2) is considered. In both works, the interplay between p_0 and f is crucial. Indeed, the unforced model (1.2) can exhibit any one of: all solutions converging to a zero; a non-zero equilibrium, or; asymptotic divergence, see [64, Theorem 2.1]. The number p_0 is equal to the stability radius of the linear system specified by A, with perturbation structure b and k^T. Indeed, $p_0 = \min |\mu|$, where the minimum is taken over all μ such that $A + \mu bk^T$ is not exponentially stable. The larger p_0, the 'larger' the perturbation A can tolerate through b and k^T without losing exponential stability.

(b) A biological interpretation of p_0 depends on the specific context. In the setup described in [14, p. 43]: "p [p_0] is simply the establishment probability that would cause stasis in a density-independent setting [meaning $f(y) = py$ for all y]." Further, it is noted in [14, p. 44] that p_0 is also equal to the reciprocal of the inherent net reproductive number of $A + bk^T$ (in the sense of [11, p. 7]), see [14, p. 44] for more details.

(c) If f and v are bounded, and assuming that (NL1) holds, then it is straightforward to show that x given by (1.2) is bounded. Consequently, if a proportional measurement error is incurred, see (2.2), with bounded ε, then it follows that $d = \varepsilon y$ is also bounded, cf. Remark 3.2 (e). Hence, the right hand side of (3.2) is finite.

(d) Using ideas behind [31, Theorem 3.1], Theorem 4.1 may be generalized to the situation wherein (1.2) is replaced by $x^+ = Ax + BF(Kx) + v$, for $(B, K) \in \mathbb{R}_+^{n\times m} \times \mathbb{R}_+^{s\times n}$ for some $m, s \in \mathbb{N}$ and $F : \mathbb{R}_+^s \to \mathbb{R}_+^m$. Assumption (NL1) and the observer (4.1) are modified accordingly. The hypothesis (NL2) on f and p is replaced by the conjunction of

- there exists $\Gamma \in \mathbb{R}_+^{m\times s}$ such that F satisfies the estimate
$$|F(\xi_1) - F(\xi_2)| \le \Gamma|\xi_1 - \xi_2| \quad \forall\, \xi_1, \xi_2 \in \mathbb{R}_+^s\,; \tag{4.4}$$
- there exists strictly positive $\xi \in \mathbb{R}_+^s$ and $\mu \in (0, 1)$ such that
$$\xi^T K_0(I - A_0)^{-1}B\Gamma \le \mu\xi^T\,, \tag{4.5}$$
  where $A_0 := A - HC$, $K_0 := K - JC$ and Γ is as in (4.4).

We comment that (4.4)–(4.5) simplify to (NL2) when $m = s = 1$.

(e) Finally, we note that Theorem 4.1 may be altered to account for nonlinearities which are not Lipschitz, provided that the Lipschitz criterion is replaced by: there exists $\alpha > 0$ such that f is μ-Lipschitz on $[\alpha, \infty)$ with $\mu < p$, and there exists $t_0 \ge 0$ such that $k^T x(t), k^T z(t) \ge \alpha$ for all $t \ge t_0$. Under these hypotheses, the bound (3.2) in Theorem 4.1 is replaced by
$$\begin{aligned}\|x(t + t_0) - z(t + t_0)\| \le\, & M\Big(r_0^t\|x(t_0) - z(t_0)\| \\ & + \max_{t_0\le\tau\le t_0+t-1}(\|v(\tau)\| + \|d(\tau)\|)\Big) \quad \forall\, t \in \mathbb{N}\,.\end{aligned}$$
However, the time t_0 above depends in general on x_0 and z_0, and so we lose uniformity with respect to initial conditions. ♢

We next present a nonlinear version of Proposition 3.3 which seeks to address optimal observer design, in a sense we describe. The proof of Proposition 4.3 is analogous to that of Proposition 3.3, and so is omitted.

Proposition 4.3. *Given* (NLO) *and* $\gamma > 0$, *assume that* (NL1) *is satisfied. The following statements hold.*

(a) *There exists* $(H_*, j_*) \in \mathbb{R}_+^{n\times q} \times \mathbb{R}_+^q$ *such that, with* $A_0 := A - H_*C$ *and* $k_0 := k - C^T j_*$,
$$\rho\big(A_0 + \gamma bk_0^T\big) \le \rho\big((A - HC) + \gamma b(k^T - j^T C)\big) \quad \forall\, (H, j) \in \mathcal{S}_{\rm nl}\,. \tag{4.6}$$

(b) *If* C *is given by* (3.7), *then*

$$H_1 = \begin{pmatrix} A(i_1) & \dots & A(i_q) \end{pmatrix}, \quad \textit{and} \quad j_1 = \begin{pmatrix} k_{i_1} & \dots & k_{i_q} \end{pmatrix}, \tag{4.7}$$

satisfy $(H_1, j_1) \in \mathcal{S}_{\mathrm{nl}}$ *if* $(H_1, j_1) \neq 0$ *(and so* $\mathcal{S}_{\mathrm{nl}} \neq \emptyset$*), in which case* $A - H_1C \leq A - HC$ *and* $k - C^Tj_1 \leq k - C^Tj$ *for all* $(H, j) \in \mathcal{S}_{\mathrm{nl}}$. *Thus* (4.6) *holds with* $(H_*, j_*) = (H_1, j_1)$ *and, further,*

$$p(H, j) \leq p(H_1, j_1) \quad \forall\, (H, j) \in \mathcal{S}_{\mathrm{nl}}\,. \tag{4.8}$$

(c) *If* C *is given by* (3.9), *then*

$$H_2 = \begin{pmatrix} \min_{k=1,\dots,q} A_{1,i_k} \\ \vdots \\ \min_{k=1,\dots,q} A_{n,i_k} \end{pmatrix} \quad \textit{and} \quad j_2 = \min_{k=1,\dots,q} j_k, \tag{4.9}$$

satisfy $(H_2, j_2) \in \mathcal{S}_{\mathrm{nl}}$ *if* $(H_2, j_2) \neq 0$ *(and so* $\mathcal{S}_{\mathrm{nl}} \neq \emptyset$*), in which case* $A - H_2C \leq A - HC$ *and* $k - C^Tj_2 \leq k - C^Tj$ *for all* $(H, j) \in \mathcal{S}_{\mathrm{nl}}$.

Thus (4.6) *holds with* $(H_*, j_*) = (H_2, j_2)$*, and* (4.8) *holds with* (H_1, j_1) *replaced by* (H_2, j_2).

Proposition 4.3 provides a recipe for how to optimally choose $(H, j) \in \mathcal{S}_{\mathrm{nl}}$ in two ecologically realistic scenarios, that is, when C is given by (3.7) or (3.9). The optimality of (H_i, j_i) in statements (b) and (c) is twofold. First, these choices minimize $\rho(A_0 + \mu b k_0^T)$, which appears in the upper bound for the error (3.2), providing a faster-decaying estimate. Second, in light of (4.8), they maximize p over $\mathcal{S}_{\mathrm{nl}}$, which enlarges (in the sense of a larger Lipschitz constant) the set of functions f to which Theorem 4.1 applies. Indeed, if $p(H_i, j_i)$ is not finite, then assumption (NL2) holds for any Lipschitz function f.

Remark 4.4. We conclude this section by commenting that in the context of observer design, a well-known and celebrated alternative is the so-called Kalman filter, introduced by Kalman in [36] in a stochastic framework for recursive state estimation, see more recently [9, Chapter 2] for instance. The Kalman filter in part motivated what is now known in control theory as H^2 optimal control, see [65, Chapter 11], and provides an estimate of (1.1) that minimizes the variance of the error over a large set of possible estimates, but this depends on both the forcing term $v(t)$ and the measurement error $d(t)$ being zero-mean white noise with gaussian distribution. Specifically, a forcing term that has gaussian distribution is highly restrictive, and may not be a suitable assumption to make in ecological models. Consequently, we have not adopted this approach.

Further, the extended Kalman filter, which is an application of the classical Kalman filter to a nonlinear system by linearizing the nonlinearity (see, for instance, [9, Chapter 7]) is known to make error estimates for situations where zero is not globally asymptotically stable in mean. This can be particularly disadvantageous in the instance that the population approaches a nonzero stable equilibrium, since the extended Kalman filter may give estimates that vary widely away from the equilibrium. Examples of Kalman filters and extened Kalman filters applied to noisy stage-structured populations can be found in [50]. ◊

5. Examples.

We present examples of observer design for linear (1.1) and nonlinear (1.2) models in Sections 5.1 and 5.2, respectively.

5.1. **Linear Examples.**

Example 5.1. We consider the age-structured matrix PPM proposed in [10] to model female cheetahs in the Serengetti. In this model, one time-step is six months and there are $n = 8$ stage-classes (0-6 months, 6-12 months, and so on, with the eighth stage comprising adults which are 42 months or older). The last four stage-classes comprise fecund adults, whilst the first four represent non-reproducing juveniles. A growth and survival matrix A is given in [10, Table 2.], where $\rho(A) = 0.955$, and so the unforced ($v = 0$) model predicts that the cheetah population shall decline asymptotically.

The paper [10] does not consider observations of the model (1.1), and so we illustrate the theory of Section 3 by discussing some different possibilities.

If we assume that just the final stage-class is measured, so that $C = e_8^T$, then by statement (b) of Proposition 3.3, the optimal $H = H_*$ is equal to the eighth column of A. Moreover, this is the componentwise largest H such that $A - HC \geq 0$. To see what this means in practice, since $A_0 = A - H_*C$ is a copy of A with zero last column and, by (3.1),

$$z^+ = A_0 z + H_* C x = A_0 z + H x_8 + H d\,,$$

we see that the final stage-class of the estimated state $z(t)$ is replaced by the measured value of the eighth stage-class $x_8(t) + d(t)$ to compute $z(t+1)$. A calculation shows that $\rho(A - H_*C) = 0.7227$ and Figure 5.1 contains an illustrative numerical simulation. For simplicity we choose zero initial observer state, $z^0 = 0$, and a randomly distributed initial population of 30 individuals. At each time step, the forcing term $v(t)$ was drawn from a discrete uniform random variable with values in $\{0, 1, 2\}$, and v is assumed to effect the first stage-class only. Proportional measurement noise of the form (2.2) is assumed, and $\varepsilon(t)$ was drawn from a truncated normally distributed random variable between -0.2 and 0.2, corresponding to a relative observation error of up to 20% at each time step. These terms were chosen for the purpose of illustration.

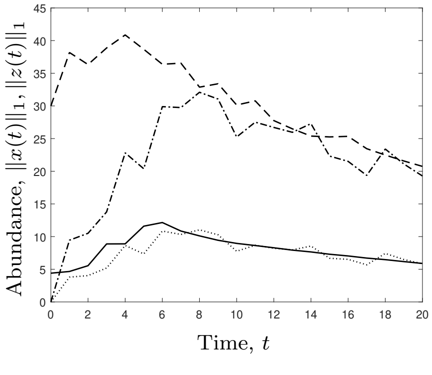


Figure 5.1. Numerical simulations from Example 5.1. Abundances from the model (LO) are plotted against time. The solid line and dotted lines are the abundance of the eighth stage-class $x_8(t)$ of the (forced) cheetah population, and its corresponding observer state $z_8(t)$, respectively. The dashed and dashed-dotted lines are $\|x(t)\|_1$ and $\|z(t)\|_1$, the total population and its observer estimate, respectively.

If instead we assume that the sum of the four adult stage-classes is observed, then $C = e_4^T + \cdots + e_8^T$. By statement (c) of Proposition 3.3, we have that $H_* = 1.143e_1$ is optimal, and $\rho(A - H_*C) = 0.8920$. Notice that observing a collection of multiple stage-classes together has led to a optimal observer with a worse (that is, greater) exponential rate of convergence.

We conclude the first example by noting that our key hypothesis (L) may not always be satisfied. Indeed, with

$$C = \begin{pmatrix} 0 & 0 & 0 & 1 & 1 & 1 & 1 & 1 \end{pmatrix},$$

which corresponds to measuring the sum of all four adult stage-classes and the final juvenile stage-class, it can be easily shown that the set $\mathcal{S}_1$ is empty. In other words, there are no non-zero $H \in \mathbb{R}_+^n$ such that $0 \leq A - HC$ and $\rho(A - HC) < 1$. ◊

5.2. **Nonlinear Examples.** A density-dependent model of the form (1.2) for Chinook salmon was analyzed in [64], using time steps in years and $n = 5$ stages, where the third, fourth, and fifth stage represented spawning adult fish while the first and second stages represented juvenile fish that do not yet spawn. The A and b terms in (1.2) are given by

$$A = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 \\ 0.0131 & 0 & 0 & 0 & 0 \\ 0 & 0.8 & 0 & 0 & 0 \\ 0 & 0 & 0.7896 & 0 & 0 \\ 0 & 0 & 0 & 0.6728 & 0 \end{pmatrix}, \quad b = \begin{pmatrix} 1 \\ 0 \\ 0 \\ 0 \\ 0 \end{pmatrix}. \tag{5.1}$$

This example is an exemplar for Lur'e systems in population ecology: A is the matrix of transition probabilities, the structure of b yields that new individuals are added into the first stage-class, and $f(k^T x(t))$ captures density-dependent recruitment. Clearly, $\rho(A) = 0 < 1$ as $A^5 = 0$, that is, A is nilpotent. We consider two different functional forms for f in Examples 5.2 and 5.3 below.

Throughout we assume that stages four and five are observed, leading to

$$C = \begin{pmatrix} 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 1 \end{pmatrix}.$$

Example 5.2. Here we assume that the nonlinear term $f : \mathbb{R}_+ \to \mathbb{R}_+$ and $k \in \mathbb{R}_+^5$ are given by

$$f(w) = \frac{30w}{8 + w} \quad \forall\, w \geq 0 \quad \text{and} \quad k^T = \begin{pmatrix} 0 & 0 & 6.524 & 100.314 & 793.294 \end{pmatrix}, \tag{5.2}$$

and so f is a so-called Beverton-Holt function. Assumption (NL1) is evidently satisfied. An application of [64, Theorem 2.1, statement 3.] yields that, for all nonzero x_0, the state x of the unforced ($v = 0$) model (1.2) with model data (5.1) and (5.2) satisfies

$$x(t) \to x^* = (I - A)^{-1} b p_0 y^* \neq 0 \quad \text{as } t \to \infty,$$

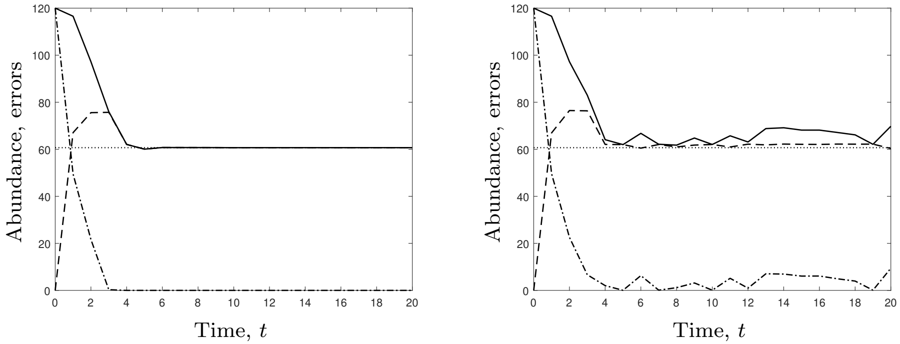
where y^* is the unique positive solution to

$$f(w) = p_0 w \quad w \geq 0\,.$$

We choose $(H, j) \in \mathcal{S}_{\mathrm{nl}}$ in accordance with statement (b) of Proposition 4.3. Since

$$0 \leq f'(w) \leq \lim_{\xi \searrow 0} \frac{f(\xi)}{\xi} = \frac{30}{8} = 3.75 < 14.6 = p(H, j) \quad \forall\, w \geq 0\,,$$

(where $f'(0)$ is the right derivative of f at 0) it follows that assumption (NL2) is satisfied. Hence, Theorem 4.1 applies to the nonlinear observed system (NLO) with model data (5.1) and (5.2). An illustrative numerical simulation is contained in Figure 5.2. In both panels we chose zero initial observer state, $z^0 = 0$, and a randomly distributed initial population of 120 individuals. Figure 5.2 (a) shows the convergence of the observer to the unknown population in the unforced case ($v = 0$ and $d = 0$). Figure 5.2 (b) illustrates the effects of nonzero disturbances. Namely, for this simulation, at each time step, the forcing term $v(t)$ was drawn from a discrete uniform random variable with integer values between 0 and 10, and is assumed to effect the final stage-class only. Proportional measurement noise of the form (2.2) is assumed, and $\varepsilon(t)$ was drawn from a truncated normally distributed random variable between -0.2 and 0.2, corresponding to a relative observation error of up to 20% at each time step in each measurement. These terms were chosen for the purpose of illustration. We see that exact asymptotic estimation is not obtained, but the error is small (of the same order of the forcing term $v(t)$). ◊



(a) Unforced

(b) Forced

Figure 5.2. Numerical simulations from Example 5.2. In both panels, the solid, dashed, dashed-dotted and dotted lines denote the total population $\|x(t)\|_1$, the corresponding estimate $\|z(t)\|_1$, the error $\|x(t) - z(t)\|_1$ and the unforced equilibrium $\|x^*\|_1$, respectively, each plotted against time t. In (a), no forcing terms are present, so $d = 0$ and $v = 0$, and the error converges to zero. In (b), the forcing and measurement error terms are nonzero, described in the main text.

Example 5.3. Now we assume that the nonlinear term $f : \mathbb{R}_+ \to \mathbb{R}_+$ and $k \in \mathbb{R}^5_+$ are given by

$$f(w) = we^{-w/10} \quad \forall\, w \geq 0 \quad \text{and} \quad k^T = \begin{pmatrix} 0 & 0 & 6.524 & 100.314 & 1400 \end{pmatrix}\,, \tag{5.3}$$

and so f is a so-called Ricker function. With these alterations, the state x of the unforced ($v = 0$) model (1.2) with model data (5.1) and (5.3) is seen numerically to oscillate for nonzero x_0. Note that assumption (NL1) still holds with k as in (5.3).

Since $|f'(w)| \leq 1$ for all $w > 0$, it follows immediately that f is 1-Lipschitz. Again we choose $(H, j) \in \mathcal{S}_{\mathrm{nl}}$ in accordance with statement (b) of Proposition 4.3, yielding $p(H, j) = 14.6$. In particular, (NL2) holds, and so Theorem 4.1 applies to the nonlinear observed system (NLO) with model data (5.1) and (5.3). An illustrative numerical simulation is contained in Figure 5.3. Here we seek to illustrate the effect of increasing measurement errors and so, for simplicity, have chosen zero additive forcing $v(t)$, and a fixed nonzero initial population x^0. In the three numerical simulations shown in Figure 5.3, a relative observation error of up to 5%, 20% and 40% was incurred at each time-step and in each stage-class, respectively. At each time-step, the error was drawn from a truncated normal distribution. We see that, as expected, larger observation errors lead to larger errors in estimation. $\diamondsuit$

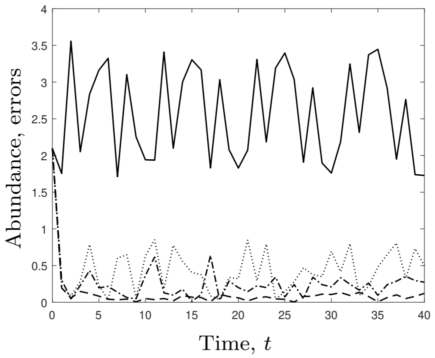


Figure 5.3. Numerical simulations from Example 5.3. The solid line denotes $\|x(t)\|_1$, and the dashed, dashed-dotted, and dotted lines denote the errors $\|x(t) - z(t)\|_1$ for increasing measurement error. See the main text.

6. **Robustness with respect to model uncertainty.**

In this penultimate section, we briefly discuss robustness of the observers considered with respect to model uncertainty, germane to observer design in an ecological setting. This problem and its solution are considered in more detail in the doctoral thesis [50].

So far we have been assuming that only the initial population distribution x^0 in the models (1.1) and (1.2) is unknown, and that the model parameters are known. In all likelihood, even if there is a "true" model of the form (1.1) or (1.2) for x, it is not likely to be known exactly, and hence subject to some so-called model uncertainty. Here we describe the robustness the observers considered have with respect to model uncertainty.

Suppose that the linear matrix PPM (1.1) is replaced by

$$x(t+1) = (A + \Delta A)x(t) + v(t), \quad x(0) = x_0, \quad t = 0, 1, 2, \dots, \tag{6.1}$$

where $A \in \mathbb{R}_+^{n \times n}$ is known, and $\Delta A \in \mathbb{R}^{n \times n}$ is unknown, but (hopefully) small. With z still given by (LO), as ΔA is not available for observer design, the observer error $e := x - z$ satisfies

$$e^+ = x^+ - z^+ = A_0 e + v - Hd + \Delta A x \,.$$

Thus, under assumption (L), it follows that, for all $t \in \mathbb{N}$,

$$\|x(t) - z(t)\| \leq M\Big(r_0^t\|x_0 - z_0\| + \max_{0 \leq \tau \leq t-1}(\|(\Delta A)x(\tau)\| + \|v(\tau)\| + \|d(\tau)\|)\Big), \quad (6.2)$$

where $H \in \mathcal{S}_1$ and r_0, M are as in Proposition 3.1. If $x(t)$ is bounded and ΔA is "small", then the bound for the difference $\|x(t) - z(t)\|$ increases by a "small" amount compared to the case when $\Delta A = 0$. Of course, in the (not ecologically realistic) situation wherein $\|x(t)\| \to \infty$ as $t \to \infty$, then it is possible that $\|(\Delta A)x(t)\| \to \infty$ as $t \to \infty$, and the bound (6.2) is uninformative. This is another shortcoming of the linear model (1.1) or (6.1) — when $\|x(t)\|$ is growing without bound, we see that uncertainties propagate through the error and prevent the observer z from providing an accurate estimate of x.

Next, consider the situation wherein the nonlinear model (1.2) is replaced by

$$x(t+1) = (A + \Delta A)x(t) + bf(k^T x(t)) + v(t), \quad x(0) = x_0, \quad t = 0, 1, 2, \ldots, \quad (6.3)$$

with analogous interpretations of the terms involved, and let z be given by (4.1). If (NL1) and (NL2) hold (the former applied to $A + \Delta A$), then estimate (6.2) again holds. In the nonlinear setting, the solution x of (6.3) is bounded under ecologically reasonable assumptions, see Remark 4.2. Similar analysis is possible in the cases that the terms b, k and f are subject to model uncertainty, although we do not give the details here.

7. **Summary and future directions.**

Dynamic observers in the context of population ecology have been considered. The observers asymptotically estimate or reconstruct the entire (unknown) state, using a combination of a model for the state and known measurements of part of the state. We have considered situations wherein the underlying models are discrete-time, and are either assumed to be linear or have a nonlinear structure of Lur'e type. We have placed a particular emphasis on the likely scenario wherein the populations of interest are described by nonlinear models, subject to potentially persistent exogenous forcing (also interpreted as a disturbance), and measurement error is incurred.

Without further information about the forcing terms, one cannot expect dynamic observers to reconstruct the state exactly, and hence we have provided assumptions in Proposition 3.1 and Theorem 4.1 under which the bounds (3.2) and (3.3) hold in the linear and nonlinear case, respectively. The former estimate bounds the norm of the current difference between the observer and state in terms of a decaying exponential, capturing the contribution from the initial state error, and a term which is linear in the 'size' of the forcing term. Consequently, when the forcing is small, the error is small, and improves asymptotically. This is very much a worst case estimate. The latter estimate bounds the ℓ^r norm of the observer/state error in terms of the norm of the initial error and the ℓ^r norms of the disturbance, and so provides an ensemble estimate. Further commentary on these estimates is given in Remark 3.2.

In the nonlinear case, our approach has in part been inspired by incremental input-to-state stability concepts, a contemporary area of research in nonlinear control theory (see, for example [1, 26]), and our treatment permits ecological nonlinearities common to population dynamics including Beverton-Holt type and Ricker functions; the former is used in cases where the nonlinearity describes compensation and the latter for overcompensation, see [48]. Roughly, our theory places assumptions on the state/observer error dynamics, captured by the interplay between the linear components and the nonlinear term f. These requirements permit the state to exhibit a rich range of biologically meaningful dynamics not captured by linear models. Further, we have considered 'optimal' observer design in Propositions 3.3 and 4.3, which minimize the decaying exponential term in the error bounds, and solved these optimisation problems in several ecologically reasonable situations. These explicit constructions are simple and intuitive and exploit the structure of the measurements natural in population ecology.

We conclude by reiterating that the present work continues a line of enquiry by the authors in seeking to: increase the uptake of; apply; and develop new tools in mathematical control theory in the context of biological sciences, particularly ecology. The concepts of forced nonlinear dynamics, feedbacks, and control or management strategies/actions are ubiquitous in both disciplines. In particular, mathematical control theory is ideally-suited to uncertain or disturbed dynamics which, we argue, is likely to be the case in realistic ecological settings. The value of this approach has been noted by other authors, including, for instance, in the context of the adaptive management of forests [23] and the study of reservoir dynamics [47].

Finally, our study on observer design in an ecological setting connects to numerous areas, each of which could be pursued further, and we briefly mention just three. First, although we have considered discrete-time systems, where many ecological models are naturally formulated, the theory presented readily extends to a continuous-time setting. We note that measurements are typically discrete, and discrete-time models also arise from continuous-time models by evaluating the solution at discrete points. In mathematical control theory, the term *sampled-data control* broadly refers to where a continuous-time process is connected to a digital (discrete-time) device. The sampled-data literature is vast, and textbooks on the subject include [8] and [68]. A natural question raised by this work is what happens when a population which, perhaps, is already difficult to measure or cryptic [7], is only irregularly measured. Ideas from aperiodically measured sampled-data control systems, for example [54], may be relevant in this setting.

Second, the problem of observer design in an ecological setting could be reformulated as an *identifiability* problem, by viewing the unknown initial state as unknown model parameters. Identifiability is a broad term, with different meanings in different academic disciplines, see [52] for instance, and a full discussion is beyond the scope of the present contribution. Identifiability comprises both questions of whether a model structure or parameter set can be determined from measurements of that model, as well as the cycle of activity of model selection, estimation/parameterisation, and validation. In mathematical control theory, the term *systems identification* is typically used for this cycle, with textbooks including [5], [42] and [56]. Interestingly, research has been conducted into the use of systems identification in this sense in an ecological context in [34], although the overlap with the present work appears minimal.

Third, we highlight that our approach has been restricted to the assumption that a population is well-modelled by finitely-many discrete stage-classes, such as age in time-steps, or insect instars. We note that many species may be naturally stratified according to some continuous variable, for example the crown or stem diameter of plants, see [53]. The natural state-space for models of the form (1.1) or (1.2) in this setting is infinite dimensional. A class of integro-difference equations which arise in ecological modelling are the so-called integral projection models (IPMs). IPMs were introduced as a tool for ecological modelling in [17], see more recently [45], and also naturally admit a Lur'e-type nonlinear structure. Stability and incremental stability analysis for such models appears in, for example [21] and [26], respectively. Consequently, we anticipate that ideas underpinning our current presentation may apply to the observer design for these classes of models.

Acknowledgement. Chris Guiver and Stuart Townley's contribution to this work was partially supported by the UK EPSRC grant EP/I019456/1. Nathan Poppelreiter and Richard Rebarber's contribution to this work was partially supported by NSF Grant DMS-1412598. Brigitte Tenhumberg's contribution was partially supported by NSF Grant DEB 1655117 and USDA/NIFA Grant 2017-03807.

We are grateful to two anonymous reviewers whose comments helped improve the first submission of this paper.

References

[1] D. Angeli. A Lyapunov approach to incremental stability properties, *IEEE Trans. Automat. Control*, 47 (2002), 410–421.

[2] M. Arcak, and P. Kokotovic, Observer-based control of systems with slope-restricted nonlinearities, *IEEE Trans. Automat. Control*, 46 (2001), 1146–1150.

[3] A. Berman, M. Neumann, and R. J. Stern, Nonnegative matrices in dynamic systems, John Wiley & Sons Inc., New York, 1989.

[4] A. Berman and R. J. Plemmons, *Nonnegative matrices in the mathematical sciences*, SIAM, Philadelphia, 1994.

[5] G. E. P. Box, G. M. Jenkins, G. C. Reinsel, G. M. Ljung, *Time series analysis*, fifth edn., John Wiley & Sons, Inc., Hoboken, 2016.

[6] H. Caswell, *Matrix population models : construction, analysis, and interpretation*, Sinauer, Massachusetts, 2001.

[7] I. Chadès, E. McDonald-Madden, M. A. McCarthy, B. Wintle, M. Linkie, and H. P. Possingham, When to stop managing or surveying cryptic threatened species, Proc. Nat. Acad. Sci., 105 (2008), 13936–13940.

[8] T. Chen and B. Francis, *Optimal sampled-data control systems*, Communications and Control Engineering Series, Springer-Verlag London, Ltd., London, 1996.

[9] C. Chui and G. Chen, Kalman Filtering, with real-time applications, Springer-Verlag, New York, 1991.

[10] K. R. Crooks, M. A. Sanjayan, and D. F. Doak, New insights on cheetah conservation through demographic modeling, *Conservation Biology*, 12 (1998), 889–895.

[11] J. M. Cushing, *An Introduction to Structured Population Dynamics*, SIAM, Philadelphia, 1998.

[12] S. N. Dashkovskiy, D. V. Efimov and E. D. Sontag. Input-to-state stability and allied system properties, *Autom. Remote Control*, 72 (2011), 1579–1614.

[13] N. Dautrebande and G. Bastin, Positive linear observers for positive linear systems, Proceedings of the European Control Conference, 1999, 1092–1095.

[14] E.A. Eager, Modelling and analysis of population dynamics using Lur'e systems accounting for competition from adult conspecifics, *Lett. Biomath.*, 3 (2016), 41–58.

[15] E.A. Eager and R. Rebarber, Sensitivity and elasticity analysis of a Lur'e system used to model a population subject to density-dependent reproduction, *Math. Biosci.*, 282 (2016), 34–45.

[16] E.A. Eager, R. Rebarber and B. Tenhumberg. Global asymptotic stability of plant-seed bank models, *J. Math. Biology*, 69 (2014), 1–37.

[17] M. R. Easterling, S. P. Ellner and P. M. Dixon, Size-specific sensitivity: applying a new structured population model, *Ecology*, 81 (2000), 694–708.

[18] X. Fan, and M. Arcak, Observer design for systems with multivariable monotone nonlinearities, *Systems Control Lett.* 50 (2003), 319–330.

[19] L. Farina and S.Rinaldi, *Positive linear systems: Theory and Applications*, Wiley-Interscience, New York, 2000.

[20] D. Franco, C. Guiver, H. Logemann and J. Perán, Semi-global persistence and stability for a class of forced discrete-time population models, *Phys. D*, 360 (2017), 46–61.

[21] D. Franco, C. Guiver, H. Logemann & J. Perán. Boundedness, persistence and stability for classes of forced difference equations arising in population ecology, *J. Math. Biol.*, 79 (2019), 1029–1076.

[22] D. Franco, H. Logemann and J. Perán, Global stability of an age-structured population model, *Systems Control Lett.*, 65 (2014), 30–36.

[23] H. R. Heinimann, A concept in adaptive ecosystem management — an engineering perspective, *Forest Ecol. Manag.*, 259 (2010), 848–856.

[24] D. Hinrichsen and A.J. Pritchard, *Mathematical Systems Theory I*, Springer, Berlin, 2005.

[25] S. Ibrir, Circle-criterion approach to discrete-time nonlinear observer design, *Automatica*, 43, (2007), 1432–1441.

[26] M. E. Gilmore, C. Guiver, and H. Logemann, Stability and convergence properties of forced infinite-dimensional discrete-time Lur'e systems. *Int. J. Control*, (2019), 1–40.

[27] J. Gouzé, A. Rapaport, and M. Hadj-Sadok, Interval observers for uncertain biological systems, *Ecol. Modelling*, 133 (2000), 45–56.

[28] C. Guiver, D. Hodgson, and S. Townley, Positive state controllability of positive linear systems, *Systems Control Lett.*, 65 (2014), 23–29.

[29] C. Guiver, C. Edholm, Y. Jin, M. Mueller, J. Powell, R. Rebarber, B. Tenhumberg, and S. Townley, Simple adaptive control for positive linear systems with applications to pest management, *SIAM J. Appl. Math*, 76 (2016), 238–275.

[30] C. Guiver, H. Logemann, R. Rebarber, A. Bill, B. Tenhumberg, D. Hodgson, & S. Townley, Integral control for population management, *J. Math. Biol.*, 70 (2005), 1015-1063.

[31] C. Guiver, H. Logemann, and B. Rüffer, Small-gain stability theorems for positive Lur'e inclusions, *Positivity* (2018): 1–41.

[32] W. M. Haddad, V. Chellaboina and Q. Hui, *Nonnegative and compartmental dynamical systems*, Princeton University Press, Princeton, 2010.

[33] M. Z. Hadj-Sadok and J. L. Gouzé, Estimation of uncertain models of activated sludge processes with interval observers, *J. Process Control*. 11 (2001), 299–310.

[34] E. Halfon (ed), *Theoretical Systems Ecology*, Academic Press, New York, 1979.

[35] D. Hinrichsen and N. K. Son, Stability radii of positive discrete-time systems, *Internat. J. Robust Nonlinear Control*, 8 (1995).

[36] R. Kalman, A New Approach to Linear Filtering and Prediction Problems, *J. Basic Engineering (ASME)*, 82D (1960), 34-45.

[37] I. Karafyllis, and Z. P. Jiang, *Stability and stabilization of nonlinear systems*, Springer-Verlag, London, 2011.

[38] N. Keyfitz and H. Caswell, *Applied Mathematical Demography*, Springer Science+Business Media, Inc., 2005.

[39] R, Klein, N. A. Chaturvedi, J. Christensen, J. Ahmed, R. Findeisen, and A. Kojic. Electrochemical model based observer design for a lithium-ion battery, *IEEE Trans. Control Syst. Technol.*, 21 (2013), 289–301.

[40] A. J. Krener, and A. Isidori, Linearization by output injection and nonlinear observers, *Systems Control Lett.*, 3 (1983), 47–52.

[41] T. Liao and N. Huang, An observer-based approach for chaotic synchronization with applications to secure communications, *IEEE Trans. Circuits Syst. I*, 46 (1999), 1144 –1150.

[42] L. Ljung, *System identification: theory for the user*, second ed., Prentice Hall, Inc., Englewood Cliffs, 1999.

[43] D. Luenberger, An introduction to observers, *IEEE Trans. Automat. Control*, 16 (1971), 596–602.

[44] D. Luenberger, Observing the state of a linear system, *IEEE Trans. Mil. Electron*, 8 (1964), 74–80.

[45] C. Merow, J. P. Dahlgren, C. J. E. Metcalf, D. Z. Childs, M. E. Evans, E. Jongejans, S. Record, M. Rees, R. Salguero-Gómez and S.M. McMahon, Advancing population ecology with integral projection models: a practical guide, *Methods Ecol. Evol.*, 5 (2014), 99–110.

[46] W. F. Morris and D. F. Doak, Quantitative conservation biology: theory and practice of population viability analysis, Sinauer Associates Sunderland, Massachusetts, USA, 2002.

[47] M. Müller, and C. A. Sierra, Application of input to state stability to reservoir models, *Theor. Ecol.*, **10** (2017). 451–475.

[48] R.A. Myers, Stock and recruitment: generalizations about maximum reproductive rate, density dependence, and variability using meta-analytic approaches, *ICES J. Marine Science*, 58 (2001), 937-951.

[49] I. M. Navon, Data Assimilation for Numerical Weather Prediction: A Review, in *Data Assimilation for Atmospheric, Oceanic and Hydrologic Applications*, S.K. Park and L. Xu eds. Springer, Berlin, 2009.

[50] N. Poppelreiter, *Dynamic Observers for Unknown Populations*, Phd Thesis, University of Nebraska, Lincoln, 2019.

[51] M. A. Rami and F. Tadeo, Positive observation problem for linear discrete positive systems, in Proceedings of the 45th IEEE Conference on Decision and Control, IEEE (2006).

[52] P. Reichert and M. Omlin, On the usefulness of overparameterized ecological models, *Ecol. Mod.*, 95 (1997), 289–299.

[53] K. E. Rose, S. M. Louda, and M. Rees, Demographic and evolutionary impacts of native and invasive insect herbivores on cirsium canescens, *Ecology*, 86 (2005), 453–465.

[54] M. de la Sen. Non-periodic and adaptive sampling. A tutorial review, *Informatica*, 7 (1996), 175–228.

[55] H. L. Smith and H. R. Thieme, Persistence and global stability for a class of discrete time structured population models, *Discrete Contin. Dyn. Syst.*, 33 (2013), 4627–4646.

[56] T. Söderström, and P. Stoica, *System Identification*, Prentice-Hall, Inc., London, 1989.

[57] E. D. Sontag, Smooth stabilization implies coprime factorization, *IEEE Trans. Automat. Control*, 34 (1989), 435–443.

[58] E.D. Sontag, Input-to-state stability: basic concepts and results, in Nonlinear and Optimal Control Theory (ed.s P. Nistri and G. Stefani), Springer (2006).

[59] E. D. Sontag, *Mathematical control theory*, second ed., Springer-Verlag, New York, 1998.

[60] M. Soroush, Nonlinear state-observer design with application to reactors, *Chemical Engineering Science*, 52 (1997), 387–404.

[61] I. Stott, S. Townley, D. Carslake, and D. J. Hodgson, On reducibility and ergodicity of population projection matrix models, *Methods Ecol. Evol.*, 1 (2010), 242–252.

[62] F. Tadeo and M. Rami, Selection of time-after-injection in bone scanning using compartmental observers, in Proceeding of World Engineering Congress, WCE (2010).

[63] B. Tenhumberg, S. Louda, J. Eckberg, and M. Takahashi, Monte carlo analysys of parameter uncertainy in matrix models for the weed *Cirsium vulgare*, J. Appl. Ecol., 45 (2008), 439–447.

[64] S. Townley, R. Rebarber, and B. Tenhumberg, Feedback control systems analysis of density dependent population dynamics, *Systems Control Lett.*, 61 (2012), 309–315.

[65] H.L. Trentelman, A.A. Stoorvogel, and M. Hautus, *Control theory for linear systems*, Communications and Control Engineering Series, Springer, (2002).

[66] J. M. Van Den Hof, Positive linear observers for linear compartmental systems, *SIAM J. Control Optim.*, 36 (1998), 590-608.

[67] X.-H. Xia, and W.-B. Gao. Nonlinear observer design by observer error linearization, *SIAM J. Control Optim.*, 27 (1989), 199–216.

[68] J. I. Yuz and G. C. Goodwin, *Sampled-data models for linear and nonlinear systems*, Communications and Control Engineering Series, Springer, London, 2014.

[69] J. Zhang, X. Zhao, R. Zhang, and Y. Chen, Improved controller design for uncertain positive systems and its extension to uncertain positive switched systems. *Asian J. Control*, 20(1) (2018), 159–173.

E-mail address: `c.guiver@bath.ac.uk`

E-mail address: `nathan.poppelreiter@huskers.unl.edu`

E-mail address: `rebarber@unl.edu`

E-mail address: `btenhumberg2@unl.edu`

E-mail address: `s.b.townley@ex.ac.uk`