



Harvest timing and its population dynamic consequences in a discrete single-species model



Begoña Cid^a, Frank M. Hilker^{b,*}, Eduardo Liz^a

^aDepartamento de Matemática Aplicada II, Universidade de Vigo, 36310 Vigo, Spain

^bCentre for Mathematical Biology, Department of Mathematical Sciences, University of Bath, Bath BA2 7AY, UK

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ABSTRACT

The timing of harvesting is a key instrument in managing and exploiting biological populations and renewable resources. Yet, there is little theory on harvest timing, and even less is known about the impact of different harvest times on the stability of population dynamics, even though this may drive population variability and risk of extinction. Here, we employ the framework proposed by Seno to study how harvesting at specific moments in the reproductive season affects not only population size but also stability. For populations with overcompensation, intermediate harvest times tend to be stabilizing (by simplifying dynamics in the case of unimodal maps and by preventing bubbling in the case of bimodal maps). For populations with a strong Allee effect, however, intermediate harvest times can have a twofold effect. On the one hand, they facilitate population persistence (if harvesting effort is low). On the other hand, they provoke population extinction (if harvesting effort is high). Early harvesting, currently considered common sense to take advantage of compensatory effects, may cut into the breeding stock when the population has not yet surpassed the critical Allee threshold. The results in this paper highlight, for the first time, the crucial interplay between harvest timing and Allee effects. Moreover, they demonstrate that harvesting with the same effort but at different moments in time can dramatically alter the impact on the population.

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1. Introduction

The sustainable exploitation of natural resources is based on their capability to ‘renew’ themselves [1]. Harvest and management theory is therefore largely concerned with the population response to the removal of individuals or resources [2]. Harvest programmes can differ in their quota or effort, i.e. the number of individuals or proportion of the population taken, but also in their selectiveness by targeting certain spatial areas, sexes, or age and size groups.

A key question of both theoretical and applied interest is the timing of the harvest (or other forms of interventions). For example, marine resources such as fish stocks may be protected from overexploitation by temporary closures of fisheries. In terrestrial ecosystems, large herbivore populations have been expanding across Europe and North America, and they are often managed during specified hunting seasons. Another, particularly illuminating example are species with distinctly seasonal dynamics such as migratory birds, which may be hunted in their wintering or breed-

ing grounds [3]. The management of waterfowl in North America has a long tradition and is well documented in the literature [4–6]. One of the reasons for this research interest is the following: If any management or harvesting programme is to take advantage of population compensation, the timing of interventions relative to density-dependent processes is essential [7,1,2].

A prevailing view and the usual practice in wildlife management is that harvesting should occur after breeding and precede periods of high natural mortality, i.e. early in the autumn [3,8]. This is because the population may compensate the removal of individuals by increased survival (compensatory mortality) or increased productivity (compensatory natality), e.g. due to less competition for resources. Removing individuals early thus improves conditions for the remaining ones and allows them to gain greater reproductive value. Also, in cervid management harvesting juveniles (or males) rather than adult females is considered not only to retain a high yield (and thus population size), but also to dampen the variance in the yield (and thus population variability). However, hunters are often reluctant to shoot juveniles (“hunting Bambi”), and the scientific evidence is scattered (see the review by Milner et al. [9] and references therein).

In the theoretical literature, little is known about the role of harvest timing [10,11,7,3]. The order of harvesting in relation to other events within the life cycle has been shown to profoundly impact the population [12,13,7,3,1,14–16]. This points out

* Corresponding author. Current address: Institute of Environmental Systems Research, Department of Mathematics and Computer Science, University of Osnabrück, 49069 Osnabrück, Germany.

E-mail addresses: beego@dma.uvigo.es (B. Cid), f.hilker@bath.ac.uk (F.M. Hilker), eliz@dma.uvigo.es (E. Liz).

the potential importance of the harvest *timing*. Yet, we know of only three studies [7,17,18] that allow for variable harvest timings at specific moments in the seasons. The mathematical models in these references are ‘semi-discrete’ in time, that is, they couple continuous processes with discrete events, thus giving rise to hybrid differential equations with periodic or impulsive functions. Moreover, they respectively consider constant yield harvesting, stage structure and environmental fluctuations, which further complicate the models. Here, we employ a simple mathematical model that has been recently proposed by Seno ([19], see also [20,21]). It is based on a single difference equation and yet allows to study the impact of harvest timing.

The Seno model considers constant effort harvesting (sometimes also called proportional harvesting), which is one of the most usual strategies in fisheries [22,23] and pest control [24,19,25]. Many authors have studied the effects of constant effort harvesting on population size in discrete-time models with overcompensatory population dynamics; see, e.g., [26,1,14,13,3,7,27,19,23,25]. Most of these papers focus on the paradoxical increase of population size in response to an increasing mortality (hydra effect) [26,28].

When taking into account the harvest timing, the Seno model predicts that compensatory effects on population size are the larger the earlier the harvesting takes place. It thus arrives at the same conclusion as other models [7,1,3,2]. However, population size is not the only important factor for a sustainable management of an exploited population or for the control of a pest species. Another key point is the stability and degree of complexity of the system; population fluctuations can make the population more prone to extinction by stochastic events, especially in small populations [29].

Although harvesting usually has a stabilizing effect on population dynamics [30,31,13], some recent empirical studies demonstrate the potential for increased mortality to lead to instability in plant, insect and fish populations [32,33,25]. Also, a recent theoretical paper proves that instabilities as a result of increased harvesting effort can be explained in a one-dimensional discrete model without considering external noise or changes in the demographic parameters, if survivorship of adults is allowed [27]. For discrete-time models with dimension higher than one, this phenomenon has been explored too; for example, the three-dimensional model of the flour beetle *Tribolium castaneum* analyzed by Costantino et al. [34], and the two-dimensional model employed by Zipkin et al. [35,25]. In both cases, an increasing adult mortality can destabilize the system. This phenomenon is linked to the mathematical concept of bubbling; for a precise definition, see [27, Definition 3].

An important aspect is whether the stability of the system depends on the harvest timing, and how this dependence affects the qualitative behavior of the population. In this paper, we use Seno’s model to show how the timing of harvesting can affect the stability properties of a population. One of the main conclusions of our study is that an appropriate harvest timing may avoid destabilizing effects in the population, and thus reduce the risk of extinction due to high variability of population size. We also pay special attention to the role of Allee effects, which have been completely ignored so far in this context.

2. The Seno model

Consider a discrete-time single-species population model

$$x_{n+1} = f(x_n) = x_n g(x_n), \tag{2.1}$$

where $x_n \in [0, \infty)$ is the population size at generation $n \in \mathbb{N}$. and $f, g : [0, \infty) \rightarrow \mathbb{R}$ are respectively the population production and the per-capita production. A typical example is the unimodal Ricker

map $f(x) = xe^{r(1-x)}$, with $r > 1$ [36], but we will also allow for survivorship of adults from one generation to the next (giving rise to bimodal maps) and for strong Allee effects (giving rise to multiple equilibria).

We now introduce the harvesting model proposed by Seno (see [19] and references therein). This model assumes that there is a specific season of length one, in which individuals accumulate energy for reproduction. In this paper, we will use this season interchangeably with ‘reproductive season’. Harvesting is assumed to take place at a moment θ ($0 \leq \theta \leq 1$) within the season. Before θ , the population production depends on x_n . Then the harvesting removes a fraction from the population, with $\gamma \in [0, 1)$ being the constant harvesting effort. After θ , the population production depends on $(1 - \gamma)x_n$. The population production is then assumed proportional to the time period before/after harvesting. The model reads (cf. [19, Eq. (1)]):

$$x_{n+1} = (1 - \gamma)x_n(\theta g(x_n) + (1 - \theta)g((1 - \gamma)x_n)). \tag{2.2}$$

Since $f(x) = xg(x)$, we rewrite (2.2) as

$$x_{n+1} = \theta(1 - \gamma)f(x_n) + (1 - \theta)f((1 - \gamma)x_n) := F_\theta(x_n). \tag{2.3}$$

There are two special cases. Firstly, the case $\theta = 0$ means that harvesting occurs at the beginning of the specific season, and then we get $F_0(x) = f((1 - \gamma)x)$; this case has received considerable attention ([26,37,27,23] and references therein). Second, the case $\theta = 1$ gives $F_1(x) = (1 - \gamma)f(x)$. The only difference between the cases $\theta = 0$ and $\theta = 1$ is census timing [14]. Actually, if we agree to measure the population just after reproduction, then the case $\theta = 1$ may be identified with $\theta = 0$. From a mathematical point of view, both cases exhibit the same dynamics because they are topologically conjugated [27]. From a biological point of view, the population dynamics results from the composition of only two separate processes (i.e., harvesting and reproduction), and any difference in population size only depends on when the population is sampled [12].

However, for the mathematical analysis, it is useful to have in mind the case $\theta = 1$ and to realize that every particular choice of F_θ is a convex combination of F_0 and F_1 :

$$F_\theta(x) = \theta F_1(x) + (1 - \theta)F_0(x). \tag{2.4}$$

Our main aim in this paper is to study how the harvesting time parameter θ affects the dynamics of model (2.3).

3. Compensatory models

In this section, we assume that $f(x) = xg(x)$, where g is continuously differentiable and satisfies the following conditions:

- (i) $g'(x) < 0$ for all $x > 0$.
- (ii) $g(0) > 1$.
- (iii) $\lim_{x \rightarrow \infty} g(x) = \delta < 1$.

Conditions (i)–(iii) are typical of single-species models with contest and scramble competition [38] and lead to under- and overcompensating stock–recruitment curves, respectively [22].

Our first observation is that overharvesting provokes extinction. The critical value of the harvesting effort γ is independent of the timing θ .

Proposition 3.1. *Assume that conditions (i)–(iii) hold. Then Eq. (2.3) has a (unique) positive equilibrium if and only if*

$$\gamma < \gamma^* := 1 - \frac{1}{g(0)}. \tag{3.1}$$

If $\gamma \geq \gamma^$, then all solutions of (2.3) converge to zero.*

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