

The Sixteenth Bellman Prize

The Bellman Prize was established in 1985 (see *Math. Biosc.* 77, 1985). It is named in honor of Richard Bellman, who founded *Mathematical Biosciences* in 1967, and awarded every two years for one outstanding article that had been published in the journal during a recent two-year time period, which in this case included 2014 and 2015. The award carries a cash award of \$1,250. This year's prize is particularly special, as *Mathematical Biosciences* is celebrating its 50th Anniversary. In a commemorative special issue (*Math. Biosc.* 287, 2017), the guest editors reminded us that the landscape of mathematical applications in biology has changed so incredibly much that it is almost incomparable to what Bellman faced in 1967, when he argued that addressing the complexity of biological systems mandated the customization and utilization of sophisticated mathematical and computational methods and techniques.

The Sixteenth Bellman Prize epitomizes the successful application of rigorous mathematics and computation to a highly pertinent biological phenomenon. It recognizes the article *Harvest timing and its population dynamic consequences in a discrete single-species model* (*Math. Biosc.* 248:78–87, 2014), which was authored by Begoña Cid, Eduardo Liz and Frank M. Hilker.

1. Summary

Population harvesting serves many purposes, from subsistence over recreation and commercial gain to pest control. Managers employ different harvest tactics that vary in quotas, gear restrictions, or area closures. Another key instrument is the *timing* of harvest (or any other form of intervention). The mathematical models in our paper [1] suggest that harvest timing can be crucial in the management of seasonally reproducing species. For the same effort of harvesting, choosing a different moment in time not only influences the population size, but can also radically alter stability properties and extinction risk.

A harvested population can be viewed as a complex nonlinear system, in which the harvest timing and effort are external parameters that influence the population-level processes that arise from the (inter-)actions among many individuals (e.g., birth, death, and competition). Harvesting often takes a pulse-like form that cuts into the population stock at a certain moment within the season. Mathematically, this strategy can be represented by impulsive differential equations or semi-discrete equations. A more tractable model emerges when one utilizes a heuristic approach proposed by Seno [2], which yields a simple convex combination of two difference equations.

In order to maintain a large population size, the prevailing view in wildlife management is that harvesting should occur early in the harvest season, i.e., after breeding and before periods of high natural mortality. The biological reasoning is that, simply speaking, removing individuals early improves the conditions for the remaining ones, for instance, because of decreased competition for resources. However,

population size alone is not the only aspect of population management. The stability of populations in terms of constancy (remaining unchanged) or persistence (avoiding extinction) can be of fundamental importance.

We investigated the impact of different harvest times in a suite of models that incorporate overcompensation, depensation (Allee effect), adult survival (iteroparity), and combinations thereof. The main results, obtained by a mixture of mathematical analysis and numerical simulations, are summarized below and illustrated in Fig. 1.

- 1) In the presence of nonlinear population cycles caused by overcompensation, intermediate harvest times can stabilize the population dynamics onto fixed points (solid black curve in Fig. 1) or cycles of lower periods and amplitudes. Mathematically, this phenomenon is related to period-halving bifurcations.
- 2) In the presence of strong depensation, the impact of harvest timing depends on the harvest effort and is two-fold:
 - On the one hand, for large harvest efforts, mid-season harvesting can induce extinction. This is related to a saddle-node bifurcation (solid red curve in Fig. 1). The critical effort level leading to extinction due to overexploitation depends on the harvest timing. That is, overexploitation could be prevented by a different choice of harvest timing.
 - On the other hand, for small harvest efforts, mid-season harvesting can facilitate the persistence of populations that would collapse to extinction after large peaks in population cycles if harvesting took place early or late in the season. From a dynamical systems point of view, this effect is related to a boundary collision (dashed blue curve in Fig. 1).

Later harvesting leads to a decrease in population size, provided the population dynamics is compensatory. This result is in line with previous work [2–5]. However, if there is strong depensation, it can be advantageous to delay harvesting until the population size exceeds the Allee threshold. A similar result holds in the presence of dynamical instabilities. In these cases, the relationship between population size and harvest timing is no longer monotonic and can be increasing rather than decreasing for later harvest times.

In summary, harvest timing can profoundly impact population size, variability, and persistence. It is therefore an essential instrument in the toolbox of sustainable exploitation. Similarly, intervention timing can be key in the management of wildly fluctuating populations, with applications ranging from protecting endangered and game species to controlling pests [6].

Harvest timing is also related to carry-over effects of species living in changing environments, where processes taking place in one season influence vital rates in later seasons of the same annual cycle [7–9].

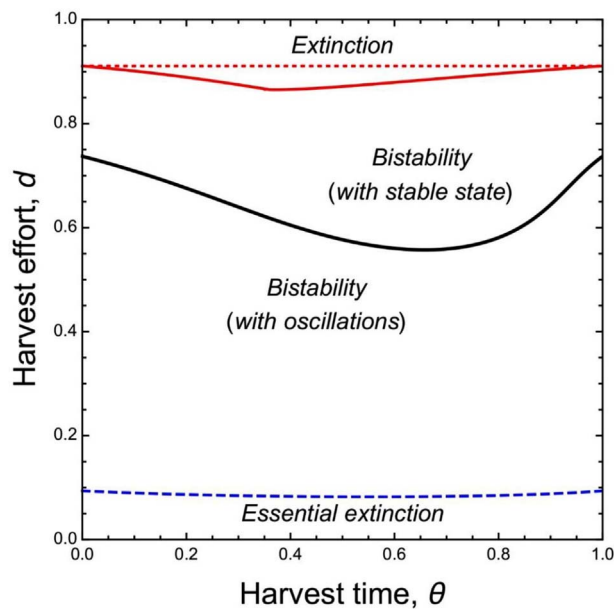


Fig. 1. Extinction and stability regions for a population model with Allee effect and overcompensation. Harvest takes place with constant effort d and at a certain time θ within the season, scaled to the unit interval. The dotted red line indicates the border to extinction caused by overharvesting when harvest timing is not accounted for (i.e., harvest taking place immediately before or after reproduction). The solid red curve shows how overharvesting becomes possible for intermediate harvest times. The dashed blue curve indicates the border to essential extinction, where a chaotic attractor disappears in a crisis. In between the red and blue curve, there is bistability. One attractor is always the extinction state, while the other one can be a stable fixed point or a periodic or chaotic cycle. The transition of the nontrivial fixed point from stability to cycles is indicated by the solid black curve. Within-season harvest timing is modeled by using the Seno model $x_{n+1} = \theta(1-d)f(x_n) + (1-\theta)f((1-d)x_n)$, where x_n is the population size in generation n , $f(x) = \frac{\alpha x^2}{1+\alpha x} \exp\{r(1-x)\}$, $\alpha = 4$ the mate search efficiency, and $r = 4$ the intrinsic per-capita production.

Work is now underway to base the model on mechanistic principles. Moreover, optimal control is currently being employed to integrate yield and cost considerations.

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The international committee selecting the winning article for the Sixteenth Bellman Prize consisted of Professors Ben Adams (University of Bath), Osvaldo Chara (Technische Universität Dresden), Adelle Coster (University of New South Wales, Sydney), Andrew Golightly (Newcastle University), Anmar Khadra (McGill University), Natalia Komarova (University of California, Irvine), Yang Kuang (Arizona State University), Mark Lewis (University of Alberta), and Necibe Tuncer (Florida Atlantic University). The committee members independently chose and ranked their top contenders among *Mathematical Biosciences* articles of 2014–2015, proposed them to the committee, and ultimately selected the award-winning article.

Eberhard O. Voit
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