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Stage-Structured Periodic Population Model for the Florida Leafwing

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Abstract. The Florida leafwing is an endemic butterfly which is distributed in South Florida and the lower Keys. Stage-structured population models are a useful tool for the management and conservation of Florida leafwing. In this work we use a discrete-time periodic control system for describing a leafwing population. One of the main differences between this model and classical stage-structured models is that in the current model we can alter the number of adults contributing to eggs production. This allows us to control the population. The solution of the problem is obtained using invariant formulations of positive periodic systems.

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1. Model description and results

Butterfly populations are in decline in Florida [5], including the Florida leafwing, *Anaea floridalis* (Nymphalidae) which is now restricted to Everglades National Park [2]. For butterflies and many other insect herbivores, at least one developmental stage in the life cycle is completely dependent on a food plant for its environment and nutrition [3]. Butterflies develop through multiple larval stages during which they feed exclusively on foliage. Following complete metamorphosis, adult butterflies emerge and either subsist on stored resources obtained as larvae or feed on liquid, sugar-rich sources available in their environment, e.g. flowers or tree sap. Conservation strategies for butterflies must therefore address the interaction of caterpillars and food plants. In recent years, several authors have used mathematical models to study species that have stage-structured lives. Structured population models allow the study of population structure, which is defined by a mix of individual attributes such as size, age, disease state, etc, [6, 9].

In this work we focus on a stage-structured model for a theoretical leafwing population that incorporates larval plant-dependent stages, and adult plant-independent stages. Leafwing caterpillars feed exclusively on plants in the genus *Croto*n, which generally occur in fire-maintained landscapes. The effects of fire and food plant on leafwing population growth are mediated through the larval stages. Leafwing butterflies feed on a variety of non-floral foods including tree sap, rotting fruit, and dung, which may contribute to their longevity as adults relative to other butterflies. In the northern range, leafwing (*Anaea andria*), have two reproductive pulses, or broods, each year, and overwinter as dormant adults [7]. In southern tropical ranges, leafwing (*A. floridalis* and other *Anaea* in the West Indies) have as many as three broods, or overlapping broods [8]. Matrix entries in our general model can be manipulated to reflect the effects of fire, different food plants, and differing numbers of broods each year. The resulting matrices can then be analyzed for population growth and stability given each hypothetical scenario. A discrete control system is used to model leafwing population growth. One of the main differences between this model and classical stage-structured models is that in the current model we can alter the number of adults contributing to eggs production. This allows us to control the population. The solution of the problem is obtained using invariant formulations of positive periodic systems.In addition, some results on stability are given.

We model a butterfly species whose life-histories is composed of a sequence within which their characteristics are broadly similar to those of other individuals in the same stage and different from those individuals in other stage. This life pattern can be split into ten distinct developmental stages, immature stages (eggs and larvae), adult stages and dormant. These different stages have different responses to environment and regulating factors to the population. We also assume that only the adult stage can reproduce and the birth rate depends on the adult population density. The state vector, $n(t) = (n_i(t))_{i=1\ldots10}$, contains the number of individuals in each stage at time t, and $n(t) \geq 0,\ \forall t \in \mathbb{N}$. By the nature of the species during summer $n_i(t) = 0, i = 1\ldots7$ and during winter $n_i(t) = 0, i = 1\cdots9$.

This model represents an entire year, making a discretization in 3-day time steps. The process is considered periodic with $T = 122$, and we consider the following parameters: $P_i(t)$ is the probability survival in stage i and stasis in i at time t; $G_i(t)$ is the probability of survival in stage i and growth from stage i to $i+1$ at time t; $R_i(t)$ is the probability of regression from stage i to $i-1$ at time t and $F(t)$ is the average contribution of egg per female at time t, taking into account that births are seasonal or occur only during a single period of the year.

Making the assumptions described above the proposed model is given by the following periodic system

$$n(t+1) = A(t)n(t) + b(t)u(t) \tag{1}$$

where $n(t) \in \mathbb{R}^{10}$ is the state vector and $u(t)$ is the control/input, $A(t)$ and $b(t)$ are real nonnegative periodic matrices of period T with appropriate dimension, i.e. $A(t+T) = A(t)$ and $b(t+T) = b(t)$. On the other hand, using the stage-structure of the population, matrix $A(t)$ is a tridiagonal matrix which has nonzero elements only in the main diagonal, $A_{ii}(t) = P_i(t)$; the first sub-diagonal, $A_{i+1i}(t) = G_i(t)$; and the first super $A_{ii+1}(t) = R_{i+1}(t)$ and $b(t)$ is a column vector which has non zero element only in the first row, $b_1(t) = 1$.

In order to study the existence and stability of equilibria of system (1) one needs a time-invariant description of the periodic system. Specifically, system (1) has associated an invariant cyclically augmented system (ICAS) (see [1] and the references given there), denoted by (A_e, B_e), as follows $z(t+1) = A_e(t)z(t) + B_e(t)u_e(t)$ where A_e is a weakly cyclic matrix of index T given by

$$\begin{pmatrix} O & A(0) \\ diag\,(A(1), \ldots, A(T-1)) & O \end{pmatrix}$$

and B_e is a block diagonal matrix whose $i-th$ diagonal block is $b(i)$. See [1] and the references given there for more details on relations between states and controls of system (1) and its ICAS.

A first step in examining a population model is to show that it is biologically feasible. It is important to establish that nonnegative initial data give rise to nonnegative solutions, that is, the population should remain nonnegative for all time $t \geq 0$. In [1] a characterization of periodic positivity is given using the ICAS associated to a periodic system. By the construction of the stage-structure model, it is straightforward to show that matrices A_e and B_e are nonnegative and this implies the positivity of periodic system (1).

Periodic systems and their solution are studied in several works. In particular, we may use these results to give an explicit solution of our model, but what really interests us is whether there exists a unique nontrivial equilibrium state.

Clearly, in our analysis the control satisfies nonnegativity, that is, $u(t) \geq 0$ and it can be interpreted as a birth function. In this work, we propose a state-feedback which represents the recruitment rate in the system, defined by

$u(t) = \lambda K(t)n(t)$ where $K(t)$ is a row vector which has non zero element only in the column 9, $K_9(t) = F(t)$ and λ is a positive constant. The periodic closed loop system is given by $n(t+1) = A_c(t)n(t)$ with $A_c(t) = A(t) + \lambda K(t)n(t)$. Note that, the state-feedback adds a new entry to the initial matrix $A(t)$ at position $(1, 9)$. And its associated ICAS formulation is given by $n_e(t+1) = A_c e(t)n_e(t)$. We want a numerical value for the equilibria, $n*$ and the stability of the system in this point. Note that "'stable"' is used here in a distinctive sense. The population itself is growing, but the relative numbers in different age classes are becoming stable.

We use the net reproductive rate or inherent net reproductive number [4], R to analize the asymptotic dynamics of the linear system. The reproductive number is the expected number of offspring per butterfly over the course of its lifetime. For obtaining R, we will use the *next generation matrix* defined as $N_G = Fe(I-T)^{-1}$, where T and Fe the transition and the fertility matrices, respectively. In our case, these matrices are given by $T = A_{ce}$ and Fe is a weakly cyclic matrix of index T, which block $f(\cdot)$ is a matrix whose only nonzero element $f_{1,9}(\cdot) = F(\cdot)$. The reproduction number is defined as the spectral radius of matrix N_G.

2. Conclusions

In this work a periodic stage-structured population with ten life stages is considered. The addition of a control input allows us to control the population. We obtain that all populations with positive initial functions tend to constant population level. In addition, the analysis of the stability of the model is given by means of the reproduction number.

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