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Separable solutions to a brood-parasite dynamics model

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Abstract

Common Cuckoo is a brood-parasite which lays its egg in the nest of other bird species and use them to raise its young. We present a Common Cuckoo and a host bird interaction deterministic model taking into account maternal care of offspring. The model consists of a coupled system of integro-partial differential equations subject to the conditions of the integral type. Number of equations in the system depends on a biologically possible maximal number of eggs of the same clutch laid by a host bird. Separable solutions of this model are studied.

1. Introduction

Brood parasites are organisms that use of host individuals either of the same or different species to raise the young of the brood-parasite. We consider the Common Cuckoo (*Cuculus canorus*), formerly European Cuckoo, and host birds interaction deterministic model. Cuckoo is a brood-parasite, which lays its eggs in the nests of other bird species, particularly of Dunnocks, Meadow Pipits, and Eurasian Reed Warblers. The cuckoo egg hatches earlier than eggs of the host bird. Cuckoo chick is much larger than its hosts [1]. It grows faster and monopolizes food supplied by the host parents [2]. Shortly after hatching it evicts all host eggs and chicks by rolling and pushing the other eggs and chicks out of the nest [2]. For the sake of simplicity we assume that it evicts all host chicks and eggs immediately after hatching and that the host bird takes care of only one cuckoo's chick living in the nest. If the hen cuckoo is out-of-phase with the host eggs, she will eat them all so that the hosts are forced to start another brood [2, 3].
In this paper, we present a common cuckoo and a host species interaction deterministic model described by a coupled system of integro-PDEs and prove the existence of its separable solutions. We take into account age of birds and a finite set of eggs in the nest and generalize a one-sex population model given in [4]. We assume that all individuals have pre-reproductive, reproductive, and post-reproductive age intervals. Individuals of reproductive age are divided into single and those who care of young offspring. Individuals of pre-reproductive age are divided into young (under maternal care) and juvenile classes. Juveniles can live without maternal care but cannot produce their offspring. It is assumed that after the death of mother all her young offspring die.
For the sake of simplicity, we consider (i) the joint parental care period which consists of the incubation and chick feeding periods and (ii) the same reproductive period for cuckoos and host birds. We also assume that the brood parasite lays his egg before incubation of clutch has started and do not take into account migration of cuckoos. To the best of our knowledge deterministic differential models have not been used yet for description of the interaction of cuckoos and host bird species.
The paper is organized as follows. In Section 2 we formulate the problem. In Section 3 we consider separable solutions of the model. Concluding remarks are given in Section 5.

2. Notation

$(0,T)$ and (T_1,T_3) $(T<T_1<T_3,\, T<T_3-T_1)$: the child care and reproductive age intervals, respectively, (the same for host birds and cuckoos),
$u(t,\tau_1)$: the age density of host birds aged τ_1 at time t who are of juvenile ($\tau_1\in(T,T_1)$), single ($\tau_1\in(T_1,T_3)$), or post-reproductive ($\tau_1>T_3$) age,
$u_k(t,\tau_1,\tau_2)$: the age density of host birds aged τ_1 at time t who take care of their k, $1\le k\le n$, offspring aged τ_2 at the same time,
$\nu(t,\tau_1)$: the natural death rate of host birds aged $\tau_1>T$ at time t who are of juvenile or adult age,

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$\nu_k(t,\tau_1,\tau_2)$: the natural death rate of host birds aged τ_1 at time t who take care of their k offspring aged τ_2,
$\nu_{ks}(t,\tau_1,\tau_2)$: the natural death rate of $k-s$ host young offspring aged τ_2 at time t whose mother is aged τ_1 at the same time,
$\alpha_k(t,\tau_1)u(t,\tau_1)d\tau_1 dt$, $\alpha_k(t,\tau_1)<1$,: the average number of host birds of age from interval $[\tau_1,\tau_1+d\tau_1]$, $\tau_1\in(T_1,T_3)$, at time t who lay k eggs in their nest in time interval $[t,t+dt]$,
$u_c(t,\tau_1,\tau_2)$: the age density of host birds aged τ_1 at time t who take care of a cuckoo chick aged τ_2,
$\nu_c(t,\tau_1,\tau_2)$: the natural death rate of host birds aged τ_1 at time t who take care of a cuckoo chick aged τ_2,
$\nu_{c0}(t,\tau_1,\tau_2)$: the natural death rate of cuckoo chick aged τ_2 at time t whose host mother is aged τ_1 at the same time,
$\alpha_{ck}(t,\tau_1)\alpha_k(t,\tau_1)u(t,\tau_1)d\tau_1 dt$, $0<\alpha_{ck}(t,\tau_1)<1$,: the average number of nests formed of one Cuckoo's and k of host bird eggs laid in time interval $[t,t+dt]$ by host birds of age from interval $[\tau_1,\tau_1+d\tau_1]$,
$f(t,\tau_c)$: the age density of Cuckoos aged τ_c at time t who are of juvenile ($\tau_c\in(T,T_1)$), reproductive ($\tau_c\in(T_1,T_3)$), or post-reproductive ($\tau_c>T_3$) age,
$\nu_f(t,\tau_c)$: the natural death rate of Cuckoos aged τ_c at time t,
$u_0(\tau_1), u_{k0}(\tau_1,\tau_2), u_{c0}(\tau_1,\tau_2), f_0(\tau_c)$: the initial age distributions,
$T_2=T_1+T$: the minimal age of an individual finishing care of offspring of the first generation,
$T_4=T_3+T$: the maximal age of an individual finishing care of offspring of the last generation,
$\alpha=\sum_{k=1}^n\alpha_k$, $\tilde{\nu}_k=\nu_k+\sum_{s=0}^{k-1}\nu_{ks}$,
$Q=\{(\tau_1,\tau_2):\tau_1\in(T_1+\tau_2,T_3+\tau_2),\ \tau_2\in(0,T)\}$.

3. The model

In this section we present a deterministic model for co-evolution of an age-structured population of host birds and cuckoos taking into account a finite number of eggs in the nest. We assume that all young offspring become juveniles at age $\tau_1=T$ and all juveniles become adults at the age $\tau_1=T_1$. Let n be the biologically possible maximal number of eggs of prey laid in the nest. Denote

$$L_1u=\partial_t u+\partial_{\tau_1}u+\nu u, \tag{3.1}$$

$$L_2z=\partial_t z+\partial_{\tau_1}z+\partial_{\tau_2}z \quad \text{for } z=u_c,u_k. \tag{3.2}$$

The model is composed of the following coupled system of integro-differential equations:

$$\begin{cases} L_2u_c+\partial_{\tau_2}u_c+(\nu_c+\nu_{c0})u_c=0, \quad (\tau_1,\tau_2)\in Q, \quad t>0,\\ u_c\big|_{\tau_2=0}=\sum\limits_{k=1}^n\alpha_{ck}\alpha_k u, \quad \tau_1\in(T_1,T_3), \quad t\ge 0,\\ u_c\big|_{t=0}=u_{c0}, \quad (\tau_1,\tau_2)\in Q, \end{cases} \tag{3.3}$$

$$\begin{cases} L_2u_n+(\nu_n+\sum\limits_{s=0}^{n-1}\nu_{ns})u_n=0, \quad (\tau_1,\tau_2)\in Q, \quad t>0,\\ L_2u_k+\big(\nu_k+\sum\limits_{s=0}^{k-1}\nu_{ks}\big)u_k\\ \qquad =\sum\limits_{s=k+1}^n\nu_{sk}u_s, \quad 1\le k\le n-1, \quad (\tau_1,\tau_2)\in Q, \quad t>0,\\ u_k\big|_{t=0}=u_{k0}, \quad (\tau_1,\tau_2)\in Q, \quad k=1,\dots,n,\\ u_k\big|_{\tau_2=0}=\alpha_k u(1-\alpha_{ck}), \quad \tau_1\in(T_1,T_3), \quad t\ge0, \quad k=1,\dots,n, \end{cases} \tag{3.4}$$

$$L_1u=\begin{cases} 0, \quad \tau_1\in(T,T_1)\cup(T_4,\infty), \quad t>0,\\ -\alpha u+\int\limits_0^{\tau_1-T_1}\big(\sum\limits_{k=1}^n\nu_{k0}u_k+\nu_{c0}u_c\big)d\tau_2, \quad \tau_1\in(T_1,T_2), \quad t>0,\\ -\alpha u+\int\limits_0^T\big(\sum\limits_{k=1}^n\nu_{k0}u_k+\nu_{c0}u_c\big)d\tau_2\\ \qquad +\big(\sum\limits_{k=1}^n u_k+u_c\big)|_{\tau_2=T}, \quad \tau_1\in(T_2,T_3), \quad t>0,\\ \int\limits_{\tau_1-T_3}^T\big(\sum\limits_{k=1}^n\nu_{k0}u_k+\nu_{c0}u_c\big)d\tau_2\\ \qquad +\big(\sum\limits_{k=1}^n u_k+u_c\big)|_{\tau_2=T}, \quad \tau_1\in(T_3,T_4), \quad t>0,\\ u\big|_{\tau_1=T}=\int\limits_{T_2}^{T_4}\sum\limits_{k=1}^n ku_k\big|_{\tau_2=T}d\tau_1, \quad t\ge0,\\ u\big|_{t=0}=u_0, \quad \tau_1\in[T,\infty),\\ u\big|_{\tau_1=T_i-0}=u\big|_{\tau_1=T_i+0}, \quad i=1,2,3,4, \quad t\ge0, \end{cases} \tag{3.5}$$

$$\begin{cases} \partial_t f + \partial_{\tau_c} f = -\nu_f f, \ \tau_c > T, t > 0, \\ f\big|_{\tau_c = T} = \int\limits_{T_2}^{T_4} u_c\big|_{\tau_2 = T} d\tau_1, \quad t \geq 0, \\ f\big|_{t=0} = f_0, \quad \tau_c \in [T, \infty). \end{cases} \tag{3.6}$$

Here ∂_t and ∂_{τ_k} signify partial derivatives. We describe fraction α_{ck} by the function

$$\alpha_{ck}(t,\tau_1) = \frac{\int\limits_{T_1}^{T_3} \beta_k(t,\tau_1,\tau_c) f(t,\tau_c) d\tau_c}{\int\limits_{T_1}^{T_3} f(t,\tau_c) d\tau_c}. \tag{3.7}$$

The first term on the right-hand side in Eq. (3.5) is conditioned by individuals who produces offspring, the second and third terms are conditioned by individuals whose all young offspring die and who finish child care, respectively. The transition term $\sum\limits_{s=0}^{k-1} \nu_{ks} u_k$ on the left-hand side in Eq. (3.4) is conditioned by individuals aged τ_1 at time t who take care of k young offspring and whose at least one young offspring dies. Similarly, the term on the right-hand side in this equation is conditioned by individuals aged τ_1 at time t who take care of more than $k, 1 \leq k \leq n-1$, young offspring aged τ_2 whose number after the death of the other offspring is equal to k. As follows from the foregoing, the given functions $\nu, \nu_k, \nu_{ks}, \nu_c, \nu_{c0}, \nu_f, \alpha_k, \alpha_{ck}, u_0, u_{k0}, u_{c0}, f_0$ must be positive supported. Constants T, T_1, and T_3 are assumed to be given and positive. The assumptions $T < T_1$, $T < T_3 - T_1$ given in Section 2 are natural.

Densities of offspring of hosts and cuckoo we define by formulas

$$u(t,\tau_2) = \int\limits_{T_1+\tau_2}^{T_3+\tau_2} \sum_{k=1}^{n} k u_k(t,\tau_1,\tau_2) d\tau_1, \quad f(t,\tau_2) = \int\limits_{T_1+\tau_2}^{T_3+\tau_2} u_c(t,\tau_1,\tau_2) d\tau_1 \tag{3.8}$$

where $\tau_2 \in [0,T]$.

4. Separable solutions to problem (1)–(7)

In this section we restrict ourselves to the case where the vital rates $\nu, \nu_c, \nu_{c0}, \nu_f, \nu_k, \nu_{ks}, \alpha_k, \alpha_{ck}$ and β_k do not depend on t. We seek solutions of the form

$$\begin{cases} u = Uv(\tau_1)\rho(t,\tau_1,\lambda), \ v(T) = 1, \\ u_k = Uv(\tau_1 - \tau_2) v_k(\tau_1,\tau_2)\rho(t,\tau_1,\lambda), \\ u_c = Uv(\tau_1 - \tau_2) v_c(\tau_1,\tau_2)\rho(t,\tau_1,\lambda), \\ f = Uw(\tau_c)\rho(t,\tau_c,\lambda), \end{cases} \tag{4.1}$$

$$\begin{cases} u_0 = Uv(\tau_1)\rho(0,\tau_1,\lambda), \\ u_{k0} = Uv(\tau_1 - \tau_2) v_k(\tau_1,\tau_2)\rho(0,\tau_1,\lambda) \\ u_{c0} = Uv(\tau_1 - \tau_2) v_c(\tau_1,\tau_2)\rho(0,\tau_1,\lambda) \\ f_0 = Uw(\tau_c)\rho(0,\tau_c,\lambda), \end{cases} \tag{4.2}$$

where $\rho(t,\tau_1,\lambda) = \exp\{\lambda(t - \tau_1 + T)\}$, $U > 0$ is an arbitrary constant while constant λ and functions v, v_k, v_c, and w are to be determined. Obviously, separable solutions are the steady-state solutions if $\lambda = 0$, die if $\lambda < 0$, and grow if $\lambda > 0$.

Theorem 4.1. *Let ν and ν_f, β_k, α_k, and functions ν_k, ν_{ks}, ν_c, ν_{c0} be positive in domains $[T,\infty)$, $[T_1,T_3] \times [T_1,T_3]$, $[T_1,T_3]$, and $\overline{Q}$, respectively, and let $\alpha < 1$ in $[T_1,T_3]$, $\beta_k < 1$ in $[T_1,T_3] \times [T_1,T_3]$.*

If $\beta_k \in C^{1,0}\big([T_1,T_3] \times [T_1,T_3]\big)$, ν_k, ν_{ks}, ν_c, and $\nu_{c0} \in C^0(\overline{Q}) \cap C^{10}(Q)$, $\alpha_k \in C^0([T_1,T_3] \cap C^1(T_1,T_3)$, ν and $\nu_f \in C^0[T,\infty)$, then system (1)–(7) has at least one class of positive separable solutions of type (4.1), (4.2).

If $\partial_{\tau_c}\beta_k = 0$ and $\beta_k \in C^0([T_1,T_3] \cap C^1((T_1,T_3))$, then system (1)–(7) has only one class of positive separable solutions of type (4.1), (4.2).

In both cases of β_k, v_c and $v_k \in C^0(\overline{Q}) \cap C^1(Q)$, $k = 1,\dots,n$, $v \in C^0([T,\infty)) \cap C^1\big((T,\infty) \setminus \{T_1,T_2,T_3,T_4\}\big)$.

Proof. Inserting Eqs. (4.1), (4.2) into (1)–(7) we derive equations for v_c, v_k, w, v,

$$\begin{cases} \partial_{\tau_1} v_c + \partial_{\tau_2} v_c + (\nu_c + \nu_{c0}) v_c = 0 \quad \text{in } Q, \\ v_c(\tau_1, 0) = \sum\limits_{k=1}^{n} \alpha_k(\tau_1) q_k(\tau_1,\lambda), \quad \tau_1 \in (T_1,T_3), \end{cases} \tag{4.3}$$

$$\begin{cases} \partial_{\tau_1} v_n + \partial_{\tau_2} v_n + \tilde{\nu}_n v_n = 0 \quad \text{in } Q, \\ \partial_{\tau_1} v_k + \partial_{\tau_2} v_k + \tilde{\nu}_k v_k = \sum\limits_{s=k+1}^{n} \nu_{sk} v_s, \quad 1 \leq k \leq n-1 \text{ in } Q, \\ v_k(\tau_1, 0) = \alpha_k(1 - q_k(\tau_1,\lambda)), \quad k = 1,\dots,n, \quad \tau_1 \in (T_1,T_3), \end{cases} \tag{4.4}$$

$$\begin{cases} w' = -\nu_f w \quad \text{in } (T,\infty) \\ w(T) = \int\limits_{T_1}^{T_3} v(x)\nu_c(x+T,T)\exp\{-\lambda x\}dx, \end{cases} \tag{4.5}$$

$$v' + \nu v = \begin{cases} 0 \quad \text{in} \quad (T,T_1)\cup(T_4,\infty), \quad v(T)=1, \\ -\alpha v + \int\limits_{T_1}^{\tau_1} K(\tau_1,\tau_1-x)v(x)dx \quad \text{in } (T_1,T_2), \\ -\alpha v + \int\limits_{\tau_1-T}^{\tau_1} K(\tau_1,\tau_1-x)v(x)dx + A(\tau_1)v(\tau_1-T) \\ \quad \text{in } (T_2,T_3), \\ \int\limits_{\tau_1-T}^{T_3} K(\tau_1,\tau_1-x)v(x)dx + A(\tau_1)v(\tau_1-T) \quad \text{in } (T_3,T_4), \\ v(T_i-0) = v(T_i+0), \quad i=1,2,3,4, \end{cases} \tag{4.6}$$

and the characteristic equation for λ,

$$\int\limits_{T_1}^{T_3} \exp\{-\lambda x\} \sum_{k=1}^{n} k\nu_k(x+T,T)v(x)dx = 1 \tag{4.7}$$

where

$$q_k(\tau_1,\lambda) = \int\limits_{T_1}^{T_3} \beta_k(\tau_1,x)w(x)\exp\{-\lambda x\}dx\Big(\int\limits_{T_1}^{T_3} w(x)\exp\{-\lambda x\}dx\Big)^{-1},$$

$$K(\tau_1,\tau_2,\lambda) = \sum_{k=1}^{n} \nu_{k0}(\tau_1,\tau_2)\nu_k(\tau_1,\tau_2) + \nu_{c0}(\tau_1,\tau_2)\nu_c(\tau_1,\tau_2),$$

$$A(\tau_1,\lambda) = \sum_{k=1}^{n} \nu_k(\tau_1,T) + \nu_c(\tau_1,T).$$

Here and in what follows the prime indicates differentiation.
We integrate Eq. (4.5) obtaining

$$w(\tau_c) = w(T)\exp\Big\{-\int\limits_{T}^{\tau_c} \nu_f(\xi)d\xi\Big\}. \tag{4.8}$$

Therefore

$$q_k(\tau_1,\lambda) = \frac{\int_{T_1}^{T_3} \beta_k(\tau_1,x)\exp\{-\lambda x - \int_T^x \nu_f(\xi)d\xi\}\,dx}{\int_{T_1}^{T_3} \exp\{-\lambda x - \int_T^x \nu_f(\xi)d\xi\}\,dx}.$$

Then integrating Eqs. (4.3) and (4.4) we determine functions ν_c and ν_n,

$$\nu_c(\tau_1,\tau_2) = \sum_{k=1}^{n} \alpha_k(\tau_1-\tau_2)q_k(\tau_1-\tau_2,\lambda)\times\exp\{-\int\limits_0^{\tau_2}(\nu_c(x+\tau_1-\tau_2,x)+\nu_{c0}(x+\tau_1-\tau_2,x))\,dx\}, \tag{4.9}$$

$$\nu_n(\tau_1,\tau_2) = \alpha_n(\tau_1-\tau_2)(1-q_n(\tau_1-\tau_2,\lambda))\exp\Big\{-\int\limits_0^{\tau_2} \tilde{\nu}_n(x+\tau_1-\tau_2,x)\,dx\Big\} \tag{4.10}$$

and derive equations for ν_k, $k=1,\ldots,n-1$,

$$\begin{aligned} \nu_k(\tau_1,\tau_2) &= \alpha_k(\tau_1-\tau_2)(1-q_k(\tau_1-\tau_2,\lambda)) \\ &\times\exp\{-\int\limits_0^{\tau_2}\tilde{\nu}_k(x+\tau_1-\tau_2,x)\,dx\} + \int\limits_0^{\tau_2}\sum_{s=k+1}^{n}(\nu_{sk}\nu_s)(y+\tau_1-\tau_2,y)\exp\{-\int\limits_y^{\tau_2}\tilde{\nu}_k(x+\tau_1-\tau_2,x)\,dx\}dy \end{aligned} \tag{4.11}$$

Equation (4.11) can be solved in the recurrent way starting with $k=n-1$ and using function (4.10). It is evident that ν_c and $\nu_k \in C^0(\overline{Q})\cap C^1(Q)$, $k=1,\ldots,n$.
Now we solve Eq. (4.6). From $(4.6)_1$ for $\tau_1\in[T,T_1]$ it follows that

$$v(\tau_1)=\exp\Big\{-\int_T^{\tau_1}\nu(\xi)\,d\xi\Big\}.$$

To determine v for $\tau_1\in(T_1,T_2]$ we integrate Eq. (4.6)$_2$ together with the initial condition $v(T_1)=\exp\{-\int_T^{T_1}\nu(\xi)\,d\xi\}$ getting

$$v(\tau_1)=v(T_1)\exp\Big\{-\int_{T_1}^{\tau_1}(\nu(\xi)+\alpha(\xi))d\xi\Big\}v(\tau_1)+\int_{T_1}^{\tau_1}\exp\Big\{-\int_y^{\tau_1}(\nu(\xi)+\alpha(\xi))d\xi\Big\}dy\int_{T_1}^{y}K(y,y-x,\lambda)v(x)dx.$$

Then changing the order of integration we reduce it to the Volterra type equation

$$\begin{cases} v(\tau_1)=v(T_1)\exp\{-\int_{T_1}^{\tau_1}(\nu(\xi)+\alpha(\xi))d\xi\} \\ \quad+\int_{T_1}^{\tau_1}v(x)dx\int_x^{\tau_1}K(y,y-x,\lambda)\exp\{-\int_y^{\tau_1}(\nu(\xi)+\alpha(\xi))d\xi\}dy \end{cases} \tag{4.12}$$

which has a unique positive solution v for any finite λ.
To determine v in $(T_2,T_3]$ we have to solve Eq. (4.6)$_3$ with the initial value $v(T_2)$ determined by Eq. (4.12). Because of the retarded structure with delay T we consider this equation going with the step T along the axis τ_1. For $\tau_1\in[T_2+sT,\min(T_2+(s+1)T,T_3))$, $s=0,1,...,$ we rewrite it in the form

$$\begin{cases} v(\tau_1)=v(T_2+sT)\exp\{-\int_{T_2+sT}^{\tau_1}\big(\nu(\xi)+\alpha(\xi)\big)d\xi\} \\ \quad+\int_{T_2+sT}^{\tau_1}\exp\{-\int_y^{\tau_1}\big(\nu(\xi)+\alpha(\xi)\big)d\xi\}dy\int_{y-T}^{y}K(y,y-x,\lambda)v(x)\,dx \\ \quad+\int_{T_2+(s-1)T}^{\tau_1-T}\exp\{-\int_{x+T}^{\tau_1}\big(\nu(\xi)+\alpha(\xi)\big)d\xi\}A(x+T,\lambda)v(x)\,dx. \end{cases} \tag{4.13}$$

Since $\{(x,y):x\in[y-T,y],\,y\in[T_2+sT,\tau_1]\}=D_1\cup D_2\cup D_3$,
where

$$\begin{aligned} D_1&=\{(x,y):x\in[y-T,\tau_1-T],\,y\in[T_2+sT,\tau_1]\}\\ &=\{(x,y):x\in[T_2+(s-1)T,\tau_1-T],\,y\in[T_2+sT,x+T]\},\\ D_2&=\{(x,y);x\in[\tau_1-T,T_2+sT],\,y\in[T_2+sT,\tau_1]\},\\ D_3&=\{(x,y):x\in[T_2+sT,y],y\in[T_2+sT,\tau_1]\}\\ &=\{(x,y):x\in[T_2+sT,\tau_1],\,y\in[x,\tau_1]\}, \end{aligned}$$

the second term in the right-hand side of Eq. (4.13) can be written as follows:

$$\begin{aligned} &\int_{T_2+sT}^{\tau_1}\exp\Big\{-\int_y^{\tau_1}(\nu(\xi)+\alpha(\xi))d\xi\Big\}dy\int_{y-T}^{y}K(y,y-x,\lambda)v(x)dx\\ &=\int_{T_2+(s-1)T}^{\tau_1-T}v(x)dx\int_{T_2+sT}^{x+T}K(y,y-x,\lambda)\exp\Big\{-\int_y^{\tau_1}(\nu(\xi)+\alpha(\xi))d\xi\Big\}dy\\ &+\int_{\tau_1-T}^{T_2+sT}v(x)dx\int_{T_2+sT}^{\tau_1}K(y,y-x,\lambda)\exp\Big\{-\int_y^{\tau_1}(\nu(\xi)+\alpha(\xi))d\xi\Big\}dy\\ &+\int_{T_2+sT}^{\tau_1}v(x)dx\int_x^{\tau_1}K(y,y-x,\lambda)\exp\Big\{-\int_y^{\tau_1}(\nu(\xi)+\alpha(\xi))d\xi\Big\}dy. \end{aligned}$$

Denote

$$\begin{aligned} g_s(\tau_1,\lambda)=&\,v(T_2+sT)\exp\Big\{-\int_{T_2+sT}^{\tau_1}(\nu(\xi)+\alpha(\xi))d\xi\Big\}+\int_{T_2+(s-1)T}^{\tau_1-T}A(x+T)v(x)\exp\Big\{-\int_{x+T}^{\tau_1}(\nu(\xi)+\alpha(\xi))\Big\}d\xi\\ &+\int_{T_2+(s-1)T}^{\tau_1-T}v(x)dx\int_{T_2+sT}^{x+T}K(y,y-x,\lambda)\exp\Big\{-\int_y^{\tau_1}(\nu(\xi)+\alpha(\xi))d\xi\Big\}dy\\ &+\int_{\tau_1-T}^{T_2+sT}v(x)dx\int_{T_2+sT}^{\tau_1}K(y,y-x,\lambda)\exp\Big\{-\int_y^{\tau_1}(\nu(\xi)+\alpha(\xi))d\xi\Big\}dy \end{aligned}$$

and rewrite Eq. (4.13) in the Volterra form

$$v(\tau_1) = g_s(\tau_1,\lambda) + \int\limits_{T_2+sT}^{\tau_1} v(x)dx \int\limits_{x}^{\tau_1} K(y,y-x,\lambda)\exp\Big\{-\int\limits_{y}^{\tau_1}(\nu(\xi)+\alpha(\xi))d\xi\Big\}dy \tag{4.14}$$

for $\tau_1 \in [T_2+sT, \min(T_2+(s+1)T, T_3)]$.

Starting with $s=0$ and using the recurrent way we first determine $g_s(\tau_1,\lambda)$ and then solve Volterra Eq. (4.14) getting $v \in C^0([T_2,T_3])$. It is evident that $v \in C^1(T_2+sT, \min(T_2+(s+1)T, T_3))$ for every fixed s. Direct calculation shows that v' is continuous at points $T_2+sT < T_3$ with $s > 1$.

Then we solve Eq. $(4.6)_4$ for $\tau_1 \in (T_3, T_4]$ with known the right hand side to get

$$\begin{aligned} v(\tau_1) &= v(T_3)\exp\Big\{-\int\limits_{T_3}^{\tau_1}\nu(\xi)d\xi\Big\} + \int\limits_{T_3}^{\tau_1}\exp\Big\{-\int\limits_{y}^{\tau_1}\nu(\xi)d\xi\Big\}dy\int\limits_{y-T}^{T_3}K(y,y-x,\lambda)v(x)dx \\ &+ \int\limits_{T_3-T}^{\tau_1-T}\exp\Big\{-\int\limits_{y+T}^{\tau_1}\nu(\xi)d\xi\Big\}A(y+T,\lambda)v(y)dy. \end{aligned}$$

For $\tau_1 > T_4$ we solve Eq. $(4.6)_1$ to get $v(\tau_1) = v(T_4)\exp\{-\int_{T_4}^{\tau_1}\nu(\xi)d\xi\}$.

From Eqs. $(4.5)_2$ and (4.9) we get

$$w(T) = \int\limits_{T_1}^{T_3} v(x)\sum_{k=1}^{n}\alpha_k(x)q_k(x,\lambda)\exp\Big\{-\lambda x - \int\limits_{0}^{T}(\nu_c(\xi,\xi)+\nu_{c0}(\xi,\xi))d\xi\Big\}dx$$

where v is determined by Eqs. (4.12) and (4.14). It is evident that

$$v \in C^0([T,\infty)) \cap C^1\big((T,\infty)\setminus\{T_1,T_2,T_3,T_4\}\big).$$

At last, inserting v_k and v determined above into Eq. (4.7) we derive an equation for λ,

$$L(\lambda) = 1,\ L(\lambda) := \int\limits_{T_1}^{T_3} e^{-\lambda x}\sum_{k=1}^{n} k v_k(x+T,T)v(x)dx. \tag{4.15}$$

If β_k is independent of τ_c, then q_k is independent of λ too. Hence, $q_k = \beta_k(\tau_1)$. Therefore, v, v_k, and v_c do not depend on λ as well. Because of the monotonicity in λ and since $L \to \infty$ as $\lambda \to -\infty$ and $L \to 0$ as $\lambda \to \infty$ Eq. (4.15) has a unique real root λ_0 such that $\lambda_0 < 0$, if $L(0) < 1$ (in this case cuckoo and host bird populations die), $\lambda_0 = 0$, if $L(0) = 1$ (both populations die), and $\lambda_0 > 0$, if $L(0) > 1$ (both populations grow).

In the case where $\partial_{\tau_c}\beta_k \neq 0$, we have

$$0 < \beta_{k*} = \min_{[T_1,T_3]\times[T_1,T_3]}\beta_k < q_k(\tau_1,\lambda) < \max_{[T_1,T_3]\times[T_1,T_3]}\beta_k = \beta_k^* < 1.$$

Let $v_c^*(\tau_1,\tau_2)$ and $v_{c*}(\tau_1,\tau_2)$ be functions defined by Eq. (4.9) with q_k replaced by β_k^* and β_{k*}, respectively. Let $v_k^*(\tau_1,\tau_2)$ and $v_{k*}(\tau_1,\tau_2)$, $k = 1,2,\ldots,n$, be functions defined by Eqs. (4.10) and (4.11) with q_k replaced by β_{k*} and β_k^*, respectively. Then $v_{c*} < v_c < v_c^*$ and $v_{k*} < v_k < v_k^*$. Hence,

$$K_*(\tau_1,\tau_2) := \sum_{k=1}^{n}\nu_{k0}(\tau_1,\tau_2)v_{k*}(\tau_1,\tau_2) + \nu_{c0}(\tau_1,\tau_2)v_{c*}(\tau_1,\tau_2) < K(\tau_1,\tau_2,\lambda)$$

$$< K^*(\tau_1,\tau_2) := \sum_{k=1}^{n}\nu_{k0}(\tau_1,\tau_2)v_k*(\tau_1,\tau_2) + \nu_{c0}(\tau_1,\tau_2)v_c*(\tau_1,\tau_2),$$

$$A_*(\tau_1) := \sum_{k=1}^{n} v_{k*}(\tau_1,T) + v_{c*}(\tau_1,T) < A(\tau_1,\lambda)$$

$$< A^*(\tau_1) := \sum_{k=1}^{n} v_k*(\tau_1,T) + v_c*(\tau_1,T).$$

Then we solve Eqs. (4.12) and (4.14) with $K(\tau_1,\tau_2,\lambda)$, $A(\tau_1,\lambda)$ replaced by $K_*(\tau_1,\tau_2)$, $A_*(\tau_1)$ and $K^*(\tau_1,\tau_2)$, $A^*(\tau_1)$ getting v_* and v^*, respectively, for $\tau_1 \in [T_1,T_3]$. Obviously, $v_* < v < v^*$.

Therefore,

$$L_*(\lambda) := \int_{T_1}^{T_3} e^{-\lambda x} \sum_{k=1}^{n} k v_{k*}(x+T,T) v_*(x) dx < L(\lambda)$$

$$< L^*(\lambda) := \int_{t_1}^{T_3} e^{-\lambda x} \sum_{k=1}^{n} k v^{k*}(x+T,T) v^*(x) dx.$$

These equations show that Eq. (4.15) has at least one real root λ. Moreover, $\lambda > 0$, if $L_*(0) > 1$, and $\lambda < 0$, if $L^*(0) < 1$. The proof is complete.

Knowing v, v_c, v_k, $k = 1, \ldots, n$, we determine densities of cuckoo and host chicks of age $\tau_2 \leq T$ by formulas (3.8),

$$f(t,\tau_2) = U \int_{T_1}^{T_3} v(x) v_c(x+\tau_2,\tau_2) \exp\{\lambda(t-x+T-\tau_2)\} dx,$$

$$u(t,\tau_2) = U \int_{T_1}^{T_3} v(x) \sum_{k=1}^{n} k v_k(x+\tau_2,\tau_2) \exp\{\lambda(t-x+T-\tau_2)\} dx.$$

5. Conclusions

The rather generic phenomenological model for Common Cuckoo interaction with the other bird species is presented. The model is composed of a system of integro-partial differential equations. All individuals have pre-reproductive, reproductive, and post-reproductive age intervals. Individuals of reproductive age are divided into single and those who care of young offspring. Individuals of pre-reproductive age are divided into young (under maternal care) and juvenile classes. Juveniles can live without maternal care but cannot produce their offspring.

In the case of special initial distributions, the existence of separable solutions of type (4.1) is proved. The conditions for the convergence of separable solutions to a steady-state solution, populations death and growth are given. The solvability of the model for the initial distributions of a general type is an open problem.

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