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Highlights

- Proposed a parasitism-mutualism-predation model with stage-structure and maturation time delays.
- Studied the existence of the positive equilibrium of three subsystems.
- Established the criteria for the global stability of the trivial equilibrium.
- Obtained the threshold dynamics for the coexistence and weak persistence.
- Studied the effect of maturation time delays on dynamics of crows and cuckoos.

ACCEPTED MANUSCRIPT

A parasitism-mutualism-predation model consisting of crows, cuckoos and cats with stage-structure and maturation delays on crows and cuckoos

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Abstract: In this paper, a parasitism-mutualism-predation model is proposed to investigate the dynamics of multi-interactions among cuckoos, crows and cats with stage-structure and maturation time delays on cuckoos and crows. The crows permit the cuckoos to parasitize their nestlings (eggs) on the crow chicks (eggs). In return, the cuckoo nestlings produce a malodorous cloacal secretion to protect the crow chicks from predation by the cats, which is apparently beneficial to both the crow and cuckoo population. The multi-interactions, i.e., parasitism and mutualism between the cuckoos (nestlings) and crows (chicks), predation between the cats and crow chicks are modeled both by Holling-type II and Beddington-DeAngelis-type functional responses. The existence of positive equilibria of three subsystems of the model are discussed. The criteria for the global stability of the trivial equilibrium are established by the Krein-Rutman Theorem and other analysis methods. Moreover, the threshold dynamics for the coexistence and weak persistence of the model are obtained, and we show, both analytically and numerically, that the stabilities of the interior equilibria may change with the increasing maturation time delays. We find there exists an evident difference in the dynamical properties of the parasitism-mutualism-predation model based on whether or not we consider the effects of stage-structure and maturation time delays on cuckoos and crows. Inclusion of stage structure results in many varied dynamical complexities which are difficult to encompass without this inclusion.

Keywords: Stage-structure; Global stability; Threshold dynamics; Coexistence; Weak persistence.

1 Introduction

In real ecosystems, there are many kinds of interactions between organisms, e.g., predation, competition, cooperation, mutualism, commensalism, parasitism and so on. Study of the dynamics of various relations among species is one of the major fields of theoretical ecology as well as of applied mathematics,

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including development of mathematical models to better understand these various interactional dynamics (e.g. Canestarin et al., 2008; Lima, 1998; Holt, 1977; Johnson et al., 1997; Rosenzweig and MacArthur, 1963; Schoener, 1983; Yoshida et al., 2003). Lotka (1925) and Volterra (1926) first proposed the predator-prey model to study the interactions between species, which is the well-known Lotka-Volterra model as most useful tool to describe and research interactions between species in ecosystems (e.g. Lima, 1998; Rosenzweig and MacArthur, 1963; Ruan and Xiao, 2001; Yoshida et al., 2003). Subsequently, versions of Lotka-Volterra models have been applied to competition (e.g. Cruz et al., 2016; Freedman and Waltman, 1985; Hardin, 1960; Holt, 1977; Liz and Ruizherrerera, 2016; Schoener, 1983), cooperation (Luo and Zhang, 2017), mutualism and parasitism models (e.g. Gillespie and Adler, 2013; Wang and DeAngelis, 2016).

However, in general, these different interactions of species mentioned above have been discussed separately. But we know that interactions can switch between one type, such as mutualism, and another, such as parasitism, depending on the abiotic or biotic context (Hoeksema and Bruna, 2015; Davies and Quinn, 2000; Thompson, 2005; Thompson and Cunningham, 2002). The associations of nesting birds with other species contain a spectrum of interactions (Haemig 2001). Some interactions may be commensal, such as when birds choose to nest in the vicinity of predators such as raptors (Myers, 1935) or social insects (Quinn and Ueta, 2008), which may provide protection from other predators and competitors without much risk to themselves. Other relations between species are considered purely antagonistic, such as those involving avian brood parasites and their hosts, in which hosts are forced to rear completely unrelated chicks at the cost of losing their own offspring (Davies and Quinn, 2000; Soler, 2014).

But avian interspecific brood parasitism can sometimes be more complex than simply and antagonistic relationship, and so it provides an ideal platform to study co-evolution (e.g. Feeney et al., 2014; Kilner and Langmore, 2011; Rothstein, 1990; Roldán and Soler, 2011; Soler et al., 2000; Soler, 2014; Spottiswoode et al., 2012). An example is that of the great spotted cuckoo (*Clamator glandarius*), which is a non-evictor brood parasite that lays its eggs in the nests of magpies (*Pica pica*) and carrion crows (*Corvus corone*) (Soler, 2014). A study of more than 16 years performed by Bolopo et al. (2015) and Canestrari et al. (2014) in an area of North Spain showed that the great spotted cuckoos benefit their carrion crow hosts in contexts of high predation risks. Cuckoo nestlings produce a malodorous cloacal secretion when they are grabbed, which apparently deters predators from parasitized host nests. Thus, the outcome of host-parasite relations in the great spotted cuckoo-carrion crow system would fluctuate yearly between parasitism and mutualism depending on the intensity of predation pressure (Soler et al., 2017).

Based on the study data (Bolopo et al., 2015; Canestrari et al., 2014) and the relations among crows, cuckoos and the predators of crow nests, Wang (2016) studied the following crow-cuckoo-cat system to characterize the relations among them:

$$\begin{cases} \frac{dx}{dt} = r_1x(1 - d_1x - \beta_1y - \frac{\beta_2z}{c_1 + x + c_2y}), \\ \frac{dy}{dt} = r_2y(-1 + \alpha_1x - d_2y), \\ \frac{dz}{dt} = r_3z(-1 + -\frac{\alpha_2x}{c_1 + x + c_2y}). \end{cases} \quad (1)$$

where x , y and z represent the population density of crows, cuckoos and cats, respectively; r_1 represents the intrinsic growth rate of species x ; r_i ($i = 2, 3$) is the death rates of species y and z ; d_i ($i = 1, 2$) denotes the density-dependent mortality rates of species x and y ; c_1 represents the half-saturation density of predation; c_2 is the time lost by predators due to deterrence of cuckoos; and α_i ($i = 1, 2$) represents the population growth rates species y, z , which, in part, incorporates how fast individuals mature and reproduce. Furthermore, in the system (1), the cuckoos depend upon the crows for survival, and the cats (i.e., free-ranging cats that hunt year-round but could be attracted with food) represent the predators of the crow chicks (Nogales et al., 2004) for convenience. In this model the functional response between the crows and cuckoos is assumed to be linear, and the crow-cat relation has a Holling type II functional response modified by adding a term proportional to the cuckoo population in the denominator, representing the time lost to the cats because of the cuckoo's deterrence. The authors hypothesized that the relations between the crows and cuckoos would fluctuate between parasitism and mutualism with the intensity of predation pressure from the cats. These fluctuations could also occur when the strength of deterrence varies.

Equations (1) omit an important aspect of all complex organisms, that they have life cycles in which they go different stages based on age. The activities and interactions of such organisms change according to stage of their life cycles. Inclusion of this structure is often essential, as a "population responds to environmental changes with time lags that reflect individual development" (Caswell et al., 1997). However, for the above model (1), the authors did not consider the stage structure of cuckoos and crows densities, which is critically important to their interactions. What's more, in model (1), the authors assumed that the growth rate of cuckoo chicks just relies on the crow chicks and has nothing to do with the adult cuckoos. And the authors also assumed that the growth rate of crow chicks is a positive constant and does not vary with the number of crow adults. At the same time, in Arias-de-Reyna (1998) and Soler et al. (2001), the authors pointed out that age difference between great spotted cuckoo and crows is an important predictor of cuckoo edging success. Canestrari et al. (2014) pointed out that, although crow nestlings are not evicted by cuckoo nestlings, the cuckoo adults will evict the crow chicks from the nest. Also, Canestrari et al. (2014) stated that the interaction of parasitism between the crows and cuckoos occurs only for the crow chicks and cuckoo nestlings; meanwhile, the predation relation between the crows and cats occurs only for the crow chicks and cat adults. Therefore, it is necessary to take the age-structure into consideration to study its effect on the dynamics of cuckoos, crows and cats. A population model including a stage-structure and size-structure is therefore one of the classical ways to study life histories (Aiello and Freedman, 1990).

From reviewing the research on population dynamics with stage-structure, we noted several studies on the dynamics of predators and their functional responses. Gourley and Kuang (2004) formulated a predator-prey model with the assumption that stage-structured consumer species growth is the result of a combination of birth and death process, both of which are closely related to the dynamical supply of resources. They determined the effect of a constant maturation time delay in a stage-structured predator-prey model in which the discrete time delay is able to produce sustainable oscillatory dynamics. Enlightened by the modeling methods in Gourley and Kuang (2004), Liu et al. (2006) studied the

following stage-structured predator-prey model with a Beddington-DeAngelis functional response type

$$\begin{cases} \frac{dx}{dt} = rx(t)\left(1 - \frac{x(t)}{K}\right) - \frac{bx(t)y(t)}{1 + k_1x(t) + k_2y(t)}, \\ \frac{dy}{dt} = \frac{nbe^{-d_j\tau}x(t-\tau)y(t-\tau)}{1 + k_1x(t-\tau) + k_2y(t-\tau)} - d_jy(t), \\ \frac{dy_j}{dt} = \frac{nbx(t)y(t)}{1 + k_1x(t) + k_2y(t)} - \frac{nbe^{-d_j\tau}x(t-\tau)y(t-\tau)}{1 + k_1x(t-\tau) + k_2y(t-\tau)} - d_jy_j(t), \end{cases} \quad (2)$$

in which x and y represent the population density of prey and mature predator, respectively, and $y_j(t)$ denotes the immature or juvenile predator population densities. They assume that the juveniles suffer a mortality rate of d_j and take τ units of time to mature; thus, $e^{-d_j\tau}$ is the survival rate of each immature predator reaching maturity. The criteria for the existence of a positive equilibrium, the necessary and sufficient conditions for the predator extinction and permanence of the system (2) were obtained. They also showed that the stability of the interior equilibrium may switch when the maturation time delay increases.

A large body of work has been done by numerous researchers on the population relations incorporating stage-structure (e.g. Aiello et al., 1992; Aiello and Freedman, 1990; Costa et al., 2016; Chen et al., 2017; Jones et al., 2017; Rothstein 1990; Wang et al., 2016; Zhang and Zhao, 2017). However, in most of these works, the scholars supposed that the birth rate from adult to juvenile stage is a constant. Obviously, this is not reasonable because the birth rate changes with the population of adults and other natural factors. Given this, Lou et al. (2017) proposed an stage-structured model for tick population subject to seasonal effects by extending the well-known McKendrick-von Foester equation:

$$\begin{cases} \frac{\partial}{\partial t}\rho(t, a) + \frac{\partial}{\partial a}\rho(t, a) = -\mu(t, a, \int_0^\infty q(t, s)\rho(t, s)ds)\rho(t, a), \\ \rho(0, a) = \phi(a), a \geq 0, \\ \rho(t, 0) = b(t, \int_0^\infty q(t, s)\rho(t, s)ds), t \geq 0, \end{cases} \quad (3)$$

where $\rho(t, a)$ is the population density with respect to the age a at time t ; $b(t, \int_0^\infty q(t, s)\rho(t, s)ds)$ denotes the egg fecundity rate, which is dependent on time t , and the population density with a weight function $p(t, a)$; and the per-capita mortality rate $\mu(t, a, \int_0^\infty q(t, s)\rho(t, s)ds)$ varies with time t , age a and the population density with another weight function $q(t, a)$. The criteria for the existence and uniqueness of solution and global stability of the positive periodic solution were obtained for above system (3).

Motivated by the above considerations and works of Canestrari et al. (2014), Wang (2016) and Lou et al. (2017), on the one hand, we specify the birth rates of crow chicks as a function of crow adults and calculate the birth rates of the cuckoo nestlings using the theory of the conversion of biomass. On the other hand, we introduce the maturation time on cuckoos and crows to better understand the interactions among cuckoos, crows and cats. The maturation time proposed in this paper is neither the time of chick development in the nest nor time to sexual maturation. It is the time taken from eggs to when they have the ability to seek food and protect themselves away from their nests. This is closely related to

time to fledging. The reason to define the maturation time in this way mainly as follows: First, the crow chicks once they have the ability to protect themselves, they will be out of the cuckoo nestlings parasitic protection. It fits our model and it also shows that the crow chicks reach the crow adults stage. Second, there are several similar definitions, such as Liu and Beretta, 2006 and Gourley and Liu, 2014. Based on the above considerations, a parasitism-mutualism-predation model was formulated to study the impacts of the maturation time delays on the multi-interactional dynamics among cuckoos, crows and cats.

The outline of the work is as follows. Section 2 shows the derivation of the model consisting of crow chicks and adults, cuckoo nestlings and adults, and cat adults. The positivity and boundedness of solutions, existences of the equilibria of three subsystems as well as the whole system are analysed in Section 3. In Section 4, we give sufficient conditions to ensure the global stability of the trivial equilibrium (cuckoo-cat free) and weak persistence of the whole system. Numerical simulations are presented in Section 5 to corroborate our analytical results. Finally, a discussion is provided in Section 6.

2 Model derivation

Throughout this paper, the subscripts x, y and z stand for crows, cuckoos and cats, respectively. The superscripts l and a of μ , i.e., μ^l and μ^a indicate the average death rates of chicks and adults, respectively. Let $l_x(t, a)$ represent the population density of crow chicks at time t of age a . These crow chicks are parasitised by the cuckoo nestlings and preyed upon by the cat adults. According to the standard von Foerster age-structured modeling approach (Keyfite et al., 1997), we use

$$\frac{\partial l_x(t, a)}{\partial t} + \frac{\partial l_x(t, a)}{\partial a} = -u_x^l l_x(t, a) - \frac{e_1 \sigma_1 l_x(t, a) L_y(t)}{1 + h_1 e_1 \sigma_1 L_x(t)} - \frac{e_2 \sigma_2 l_x(t, a) A_z(t)}{1 + h_2 e_2 \sigma_2 L_x(t) + k_2 L_y(t)} \quad (4)$$

to show the density loss of crow chicks, either by natural deaths with an average mortality rate u_x^l or by being parasitised by the cuckoo nestlings and preyed upon by the cat adults, which are described by the second and third terms in (4), respectively. $L_x(t)$, $L_y(t)$ and $A_z(t)$ represent the (total) population of crow chicks, cuckoo nestlings and cat adults at time t , respectively. We use the Holling type II functional response $\frac{e_1 \sigma_1 l_x(t, a) L_y(t)}{1 + h_1 e_1 \sigma_1 L_x(t)}$ to characterize the parasitism between the crow chicks and cuckoos nestlings, at the same time, we use the Beddington-DeAngelis type functional response $\frac{e_2 \sigma_2 l_x(t, a) A_z(t)}{1 + h_2 e_2 \sigma_2 L_x(t) + k_2 L_y(t)}$ to show both the mutualism between the crow chicks and cuckoo nestlings, and the predation between the crow chicks and cat adults as well. The parameter $h_i (i = 1, 2)$ represents the handling (digestion) time per unit biomass consumed, and $e_i (i = 1, 2)$ represents the crow chicks biomass encounter rate with cuckoos and crows. The parameter $\sigma_i (i = 1, 2)$ is the fraction of the consumed crow chick biomass.

The total population of the crow chicks at time t is

$$L_x(t) = \int_0^{\tau_x} l_x(t, a) da, \quad (5)$$

where τ_x is the maturation time delay of crow chicks. In fact, the maturation time taken depends on many external natural factors (such as temperature, the height of nests). In view of the difficulties in modeling this dependence, we let τ_x as a known constant here. Differentiating (5) with respect to t on

both sides, and using (4), we obtain

$$\frac{dL_x(t)}{dt} = l_x(t, 0) - l_x(t, t_x) - u_x^l L_x(t) - \frac{e_1 \sigma_1 L_x(t) L_y(t)}{1 + h_1 e_1 \sigma_1 L_x(t)} - \frac{e_2 \sigma_2 L_x(t) A_z(t)}{1 + h_2 e_2 \sigma_2 L_x(t) + k_2 L_y(t)}. \quad (6)$$

Now, $l_x(t, 0)$ is the hatching rate of the crows; this is taken to be a function $B(\cdot)$ of the total number $A_x(t)$ of crow adults and it is usually a reasonable assumption to model populations from biological significance. Thus,

$$l_x(t, 0) = B(A_x(t)). \quad (7)$$

To get the specific expression of (6), we need to calculate $l_x(t, \tau_x)$. Let

$$l_x^\omega(a) = l_x(a + \omega, a). \quad (8)$$

Differentiating (8) with respect to a on both sides, and by (4), we obtain

$$\frac{dl_x^\omega(a)}{da} = -u_x^l l_x^\omega(a) - \frac{e_1 \sigma_1 l_x^\omega(a) L_y(a + \omega)}{1 + h_1 e_1 \sigma_1 L_x(a + \omega)} - \frac{e_2 \sigma_2 l_x^\omega(a) A_z(a + \omega)}{1 + h_2 e_2 \sigma_2 L_x(a + \omega) + k_2 L_y(a + \omega)},$$

so that

$$l_x^\omega(a) = l_x^\omega(0) \exp \left\{ - \int_0^a \left[u_x^l + \frac{e_1 \sigma_1 L_y(\theta + \omega)}{1 + h_1 e_1 \sigma_1 L_x(\theta + \omega)} + \frac{e_2 \sigma_2 A_z(\theta + \omega)}{1 + h_2 e_2 \sigma_2 L_x(\theta + \omega) + k_2 L_y(\theta + \omega)} \right] d\theta \right\}.$$

Let $a = \tau_x$, $\omega = t - \tau_x$, and by (7), we obtain

$$l_x(t, \tau_x) = B(A_x(t - \tau_x)) \exp \left\{ - \int_0^{\tau_x} \left[u_x^l + \frac{e_1 \sigma_1 L_y(\theta + \omega)}{1 + h_1 e_1 \sigma_1 L_x(\theta + \omega)} + \frac{e_2 \sigma_2 A_z(\theta + \omega)}{1 + h_2 e_2 \sigma_2 L_x(\theta + \omega) + k_2 L_y(\theta + \omega)} \right] d\theta \right\}. \quad (9)$$

Then, the crow chicks' specific final equation was obtained by taking (7) and (9) into (6)

$$\begin{aligned} \frac{dL_x(t)}{dt} = & -u_x^l L_x(t) - \frac{e_1 \sigma_1 L_x(t) L_y(t)}{1 + h_1 e_1 \sigma_1 L_x(t)} - \frac{e_2 \sigma_2 L_x(t) A_z(t)}{1 + h_2 e_2 \sigma_2 L_x(t) + k_2 L_y(t)} \\ & + B(A_x(t)) - B(A_x(t - \tau_x)) \exp \left\{ - \int_{t-\tau_x}^t \left[u_x^l + \frac{e_1 \sigma_1 L_y(\theta)}{1 + h_1 e_1 \sigma_1 L_x(\theta)} + \frac{e_2 \sigma_2 A_z(\theta)}{1 + h_2 e_2 \sigma_2 L_x(\theta) + k_2 L_y(\theta)} \right] d\theta \right\}, \end{aligned} \quad (10)$$

which can also be written in the integral equation form

$$L_x(t) = \int_{t-\tau_x}^t B(A_x(\xi)) \exp \left\{ - \int_\xi^t \left[u_x^l + \frac{e_1 \sigma_1 L_y(\theta)}{1 + h_1 e_1 \sigma_1 L_x(\theta)} + \frac{e_2 \sigma_2 A_z(\theta)}{1 + h_2 e_2 \sigma_2 L_x(\theta) + k_2 L_y(\theta)} \right] d\theta \right\} d\xi. \quad (11)$$

The last term in (10) is the rate at which the crow chicks mature into crow adults. In (10), the Holling type II functional response $\frac{e_1\sigma_1 L_x(t)L_y(t)}{1+h_1e_1\sigma_1 L_x(t)}$ has the term $L_x(t)$ in both its numerator and denominator so as to therefore level off at large values of $L_x(t)$. This yields the important fact that each parasitised cuckoo nestling can consume only a limited quantity of the crow chick biomass per unit time. This rather important observation means that a single crow chick offers a large amount of food for a single cuckoo nestling. Moreover, adding a term proportional to $L_y(t)$ to the denominator of the Beddington-DeAngelis type functional response represents the time lost to the cats. By (10) and (11), we may obtain an equation for the population $A_x(t)$ of crow adults from the biological fact:

$$\begin{aligned} \frac{dA_x(t)}{dt} = & -u_x^a A_x(t) + B(A_x(t - \tau_x)) \exp \left\{ - \int_{t-\tau_x}^t \left[u_x^l + \frac{e_1\sigma_1 L_y(\theta)}{1 + h_1 e_1 \sigma_1 L_x(\theta)} \right. \right. \\ & \left. \left. + \frac{e_2\sigma_2 A_z(\theta)}{1 + h_2 e_2 \sigma_2 L_x(\theta) + k_2 L_y(\theta)} \right] d\theta \right\}, \end{aligned} \quad (12)$$

where u_x^a is the the average death rate for crow adults, and other parameters have the same meaning as above.

Next, we need to derive the equations for the cuckoo nestlings and cuckoo adults. The second term in the right-hand side of (10) describes the parasitism of cuckoo nestlings and denotes the quantity of resources consumed by cuckoo nestlings. The consumed crow chicks biomass is converted into cuckoo nestlings biomass, as with any parasitism interaction, but in this case the process needs some time i.e., it is obviously not instantaneous. We compute this conversion by considering the cuckoo nestlings that mature at time t , and they mate and lay eggs soon after maturation; i.e., this is assumed to occur with only negligible delay. Suppose τ_y is the maturation time for the cuckoo nestlings. Those cuckoo nestlings that mature at time t , between time ξ and $\xi + d\xi$ with $\xi \in (t - \tau_y, t)$ consumed a quantity

$$\exp[-u_y^l(t - \xi)] \frac{e_1\sigma_1 L_x(\xi)L_y(\xi)}{1 + h_1 e_1 \sigma_1 L_x(\xi)} d\xi$$

of crow chicks biomass. The exponential term $\exp[-u_y^l(t - \xi)]$ denotes survival probability of the cuckoo nestlings over the time interval $[\xi, t]$. Ignoring it will lead to computing all crow chick biomass being consumed over the time interval $[\xi, \xi + d\xi]$, including consumption by those cuckoo nestlings that have died since. The total number of the crow chicks biomass consumed by those survived cuckoo nestlings and are ready to mature at time t is

$$\int_{t-\tau_y}^t \exp[-u_y^l(t - \xi)] \frac{e_1\sigma_1 L_x(\xi)L_y(\xi)}{1 + h_1 e_1 \sigma_1 L_x(\xi)} d\xi.$$

At time t or soon after, this crow chick biomass is converted into new cuckoo nestlings biomass in the form of a plenty of cuckoo eggs. If the above quantity is multiplied by a parameter C_1 , which measures the efficiency of this conversion, we obtain a number of eggs laid by those cuckoos that have just matured at time t . This number has to be converted into the breeding rate. The eggs might be laid over a very transient time interval after maturation in practice, or maybe even all at once, so we regard these cuckoo eggs as a flock of cuckoo nestlings that have taken a time τ_y to mature. Therefore, we divide it by τ_y and

get the hatching rate $l_y(t, 0)$ of the cuckoos

$$l_y(t, 0) = \frac{C_1}{\tau_y} \int_{t-\tau_y}^t \exp[-u_y^l(t-\xi)] \frac{e_1 \sigma_1 L_x(\xi) L_y(\xi)}{1 + h_1 e_1 \sigma_1 L_x(\xi)} d\xi, \quad (13)$$

where $l_y(t, a)$ is the age density function for the cuckoos. Since τ_y is the maturation time for the cuckoo nestlings, according to the standard von Foerster age-structured modeling approach as the same above, we have

$$\frac{\partial l_y(t, a)}{\partial t} + \frac{\partial l_y(t, a)}{\partial a} = -u_y^l l_y(t, a), \quad 0 < a < \tau_y. \quad (14)$$

Next, we calculate $l_y(t, \tau_y)$ to obtain the equation for cuckoo nestlings. Define

$$l_y^\xi(a) = l_y(a + \xi, a). \quad (15)$$

Differentiating (15) with respect to a on both sides, and by (14), we get

$$\frac{dl_y^\xi(a)}{da} = -u_y^l l_y^\xi(a)$$

so that

$$l_y^\xi(a) = l_y^\xi(0) \exp\left[-\int_0^a u_y^l d\theta\right].$$

Setting $a = \tau_y$ and $\xi = t - \tau_y$, we obtain

$$l_y(t, \tau_y) = \frac{\exp(-u_y^l \tau_y) C_1}{\tau_y} \int_{t-2\tau_y}^{t-\tau_y} \exp[-u_y^l(t-\tau_y-\xi)] \frac{e_1 \sigma_1 L_x(\xi) L_y(\xi)}{1 + h_1 e_1 \sigma_1 L_x(\xi)} d\xi \quad (16)$$

for $t > 2\tau_y$. Equation (16) implies that the rate of cuckoos' maturation at time t is the cuckoo nestlings survival probability $\exp(-u_y^l \tau_y)$ multiplied by the natality $l_y(t - \tau, 0)$ at the earlier time $t - \tau_y$. The latter relies on the quantity of crow chicks biomass consumed by the previous generation over the earlier time interval $[t - 2\tau_y, t - \tau_y]$. Having noted this explanation of (16), we combine and simplify the exponentials therein. Now

$$L_y(t) = \int_0^{\tau_y} l_y(t, a) da. \quad (17)$$

Then, by differentiating (17) with t on both sides, and by using (13) and (16) we have

$$\begin{aligned} \frac{dL_y(t)}{dt} &= -u_y^l L_y(t) + \frac{C_1}{\tau_y} \int_{t-\tau}^t \exp[-u_y^l(t-\xi)] \frac{e_1 \sigma_1 L_x(\xi) L_y(\xi)}{1 + h_1 e_1 \sigma_1 L_x(\xi)} d\xi \\ &\quad - \frac{C_1}{\tau_y} \int_{t-2\tau_y}^{t-\tau_y} \exp[-u_y^l(t-\xi)] \frac{e_1 \sigma_1 L_x(\xi) L_y(\xi)}{1 + h_1 e_1 \sigma_1 L_x(\xi)} d\xi. \end{aligned} \quad (18)$$

The following integral equation is an alternative to (18):

$$L_y(t) = \frac{C_1}{\tau_y} \int_{t-\tau_y}^t \int_{\theta-\tau_y}^{\theta} \exp[-u_y^l(t-\xi)] \frac{e_1 \sigma_1 L_x(\xi) L_y(\xi)}{1 + h_1 e_1 \sigma_1 L_x(\xi)} d\xi d\eta. \quad (19)$$

From the third term of (18), for the number $A_y(t)$ of cuckoo adults at time t , we have the following equation:

$$\frac{dA_y(t)}{dt} = -u_y^a A_y(t) + \frac{C_1}{\tau_y} \int_{t-2\tau_y}^{t-\tau_y} \exp[-u_y^l(t-\xi)] \frac{e_1 \sigma_1 L_x(\xi) L_y(\xi)}{1 + h_1 e_1 \sigma_1 L_x(\xi)} d\xi. \quad (20)$$

Finally, we need the equations for cat adults. From the third term of the equation (10), we obtain

$$\frac{dA_z(t)}{dt} = -u_z^a(t) A_z(t) + \frac{C_2 e_2 \sigma_2 L_x(t) A_z(t)}{1 + h_2 e_2 \sigma_2 L_x(t) + k_2 L_y(t)}. \quad (21)$$

Based on the above derivation, our complete system is as follows:

$$\left\{ \begin{array}{l} \frac{dL_x(t)}{dt} = -u_x^l L_x(t) - \frac{e_1 \sigma_1 L_x(t) L_y(t)}{1 + h_1 e_1 \sigma_1 L_x(t)} - \frac{e_2 \sigma_2 L_x(t) A_z(t)}{1 + h_2 e_2 \sigma_2 L_x(t) + k_2 L_y(t)} \\ \quad + B(A_x(t)) - B(A_x(t - \tau_x)) \exp \left\{ - \int_{t-\tau_x}^t \left[u_x^l + \frac{e_1 \sigma_1 L_y(\theta)}{1 + h_1 e_1 \sigma_1 L_x(\theta)} \right. \right. \\ \quad \left. \left. + \frac{e_2 \sigma_2 A_z(\theta)}{1 + h_2 e_2 \sigma_2 L_x(\theta) + k_2 L_y(\theta)} \right] d\theta \right\}, \\ \frac{dA_x(t)}{dt} = -u_x^a A_x(t) + B(A_x(t - \tau_x)) \exp \left\{ - \int_{t-\tau_x}^t \left[u_x^l + \frac{e_1 \sigma_1 L_y(\theta)}{1 + h_1 e_1 \sigma_1 L_x(\theta)} \right. \right. \\ \quad \left. \left. + \frac{e_2 \sigma_2 A_z(\theta)}{1 + h_2 e_2 \sigma_2 L_x(\theta) + k_2 L_y(\theta)} \right] d\theta \right\}, \\ \frac{dL_y(t)}{dt} = -u_y^l L_y(t) + \frac{C_1}{\tau_y} \int_{t-2\tau_y}^t \exp[-u_y^l(t-\xi)] \frac{e_1 \sigma_1 L_x(\xi) L_y(\xi)}{1 + h_1 e_1 \sigma_1 L_x(\xi)} d\xi \\ \quad - \frac{C_1}{\tau_y} \int_{t-2\tau_y}^{t-\tau_y} \exp[-u_y^l(t-\xi)] \frac{e_1 \sigma_1 L_x(\xi) L_y(\xi)}{1 + h_1 e_1 \sigma_1 L_x(\xi)} d\xi, \\ \frac{dA_y(t)}{dt} = -u_y^a A_y(t) + \frac{C_1}{\tau_y} \int_{t-2\tau_y}^{t-\tau_y} \exp[-u_y^l(t-\xi)] \frac{e_1 \sigma_1 L_x(\xi) L_y(\xi)}{1 + h_1 e_1 \sigma_1 L_x(\xi)} d\xi, \\ \frac{dA_z(t)}{dt} = -u_z^a(t) A_z(t) + \frac{C_2 e_2 \sigma_2 L_x(t) A_z(t)}{1 + h_2 e_2 \sigma_2 L_x(t) + k_2 L_y(t)}. \end{array} \right. \quad (22)$$

At the same time, we get the alternative to (22) for convenience

$$\left\{ \begin{array}{l} L_x(t) = \int_{t-\tau_x}^t B(A_x(\xi)) \exp \left\{ - \int_{\xi}^t \left[u_x^l + \frac{e_1 \sigma_1 L_y(\theta)}{1 + h_1 e_1 \sigma_1 L_x(\theta)} \right. \right. \\ \left. \left. + \frac{e_2 \sigma_2 A_z(\theta)}{1 + h_2 e_2 \sigma_2 L_x(\theta) + k_2 L_y(\theta)} \right] d\theta \right\} d\xi, \\ \frac{dA_x(t)}{dt} = -u_x^a A_x(t) + B(A_x(t - \tau_x)) \exp \left\{ - \int_{t-\tau_x}^t \left[u_x^l + \frac{e_1 \sigma_1 L_y(\theta)}{1 + h_1 e_1 \sigma_1 L_x(\theta)} \right. \right. \\ \left. \left. + \frac{e_2 \sigma_2 A_z(\theta)}{1 + h_2 e_2 \sigma_2 L_x(\theta) + k_2 L_y(\theta)} \right] d\theta \right\}, \\ L_y(t) = \frac{C_1}{\tau_y} \int_{t-\tau_y}^t \int_{\theta-\tau_y}^{\theta} \exp[-u_y^l(t - \xi)] \frac{e_1 \sigma_1 L_x(\xi) L_y(\xi)}{1 + h_1 e_1 \sigma_1 L_x(\xi)} d\xi d\eta, \\ \frac{dA_y(t)}{dt} = -u_y^a A_y(t) + \frac{C_1}{\tau_y} \int_{t-2\tau_y}^{t-\tau_y} \exp[-u_y^l(t - \xi)] \frac{e_1 \sigma_1 L_x(\xi) L_y(\xi)}{1 + h_1 e_1 \sigma_1 L_x(\xi)} d\xi, \\ \frac{dA_z(t)}{dt} = -u_z^a A_z(t) + \frac{C_2 e_2 \sigma_2 L_x(t) A_z(t)}{1 + h_2 e_2 \sigma_2 L_x(t) + k_2 L_y(t)}. \end{array} \right. \quad (23)$$

The two systems are equivalent for the restricted class of initial data such that (11) and (19) hold at time $t = 0$, which is also ecologically realistic.

3 Model analysis

Throughout the model analysis, we make the following assumptions on the birth rate $B(\cdot)$ of crows from the biologically acceptable points:

- (a) $B(0) = 0$, $B(A)$ is increasing and $\dot{B}(A)$ is decreasing for $A > 0$;
- (b) There exists $A_x^{**} > 0$ such that $\exp(-u_x^l \tau_x) B(A) > u_x^a A$ when $0 < A < A_x^{**}$;
- (c) $\exp(-u_x^l \tau_x) B(A) < u_x^a A$ when $A > A_x^{**}$.

Note that (24) implies

$$\dot{B}(0) \exp(-u_x^l \tau_x) > u_x^a. \quad (25)$$

Remark 3.1. From a biological point of view, the assumptions of (24) show that the birth function $B(\cdot)$ of crow chicks is density-dependent on the crow adults. Generally, the number of newly matured crow adults $\exp(-u_x^l \tau_x) B(A_x(t))$ is greater than the removed $u_x^a A_x$ when A_x is small ($A_x < A_x^{**}$), and it is opposite when A_x is large ($A_x > A_x^{**}$). Moreover, the inequality (25) is strict because $\dot{B}(A)$ is decreasing.

3.1 Positivity and boundedness.

We first prove the positivity and boundedness of solutions for the system (22) or (23).

Theorem 3.1. *Assume that assumption (24) holds, that all five variables are nonnegative and continuous on their respective initial intervals, and that (11) and (19) hold at $t = 0$. Then all components of the solution of system (22), or of the variant system (23) are nonnegative and bounded for all $t \geq 0$.*

Proof. By the system (12), we have

$$A_x(t) = A_x(0) \exp(-u_x^a t) + \int_0^t B(A_x(s - \tau_x)) \hat{K} \exp[u_x^a(s - t)] ds, \quad (26)$$

where

$$\hat{K} = \exp \left[- \int_{s-\tau_x}^s \left(u_x^l + \frac{e_1 \sigma_1 L_y(\theta)}{1 + h_1 e_1 \sigma_1 L_x(\theta)} + \frac{e_2 \sigma_2 A_z(\theta)}{1 + h_2 e_2 L_x(\theta) + k_2 L_y(\theta)} \right) d\theta \right].$$

Then we have $A_x(t) > 0$ holding for all $t \geq 0$; otherwise, there must exist $t_0 > 0$ such that $A_x(t_0) = 0$. Let $t_1 = \inf\{t_0 > 0 : A_x(t_0) = 0\}$; thus we have $A_x(t_1) = 0$ and $A_x(t) > 0$ for all $t \in [0, t_1)$. From (26), we get

$$A_x(t_1) = A_x(0) \exp(-u_x^a t_1) + \int_0^{t_1} B(A_x(s - \tau_x)) \hat{K} \exp[u_x^a(s - t_1)] ds > 0,$$

which leads to a contradiction to $A_x(t_1) = 0$. This proves the positivity of $A_x(t)$ for all $t \geq 0$.

Next, we prove that $L_x(t) > 0$ for all $t \geq 0$. By the positivity of $A_x(t)$ and the assumption (24), we can get $B(A_x(\xi)) > 0$. Then from (11), we can prove $L_x(t) > 0$ for all $t \geq 0$ by using similar arguments above.

In order to prove the positivity of $L_y(t)$, $A_y(t)$ and $A_z(t)$, we get the integral form of the equation (18), (20) and (21), respectively;

$$\begin{aligned} L_y(t) &= \frac{C_1}{\tau_y} \int_{t-\tau_y}^t \int_{\theta-\tau_y}^{\theta} \exp[-u_y^l(t-\xi)] \frac{e_1 \sigma_1 L_x(\xi) L_y(\xi)}{1 + h_1 e_1 \sigma_1 L_x(\xi)} d\xi d\theta, \\ A_y(t) &= \exp(-u_y^a t) \left[A_y(0) + \int_0^t \frac{C_1}{\tau_y} \int_{s-2\tau_y}^{s-\theta_y} \exp[-u_y^l(s-\xi)] \right. \\ &\quad \left. - u_y^a s \right] \frac{e_1 \sigma_1 L_x(\xi) L_y(\xi)}{1 + h_1 e_1 \sigma_1 L_x(\xi) + k_2 L_y(\xi)} d\xi ds, \\ A_z(t) &= A_z(0) \exp \left[\int_0^t \left(-u_z^a + \frac{C_2 e_2 \sigma_2 L_x(s)}{1 + h_2 e_2 \sigma_2 L_x(s) + k_2 L_y(s)} \right) ds \right]. \end{aligned} \quad (27)$$

Similar to the above proof, we can prove that $L_y(t) > 0$, $A_y(t) > 0$ and $A_z(t) > 0$ for all $t \geq 0$, respectively.

Then we prove the boundedness of the solutions the system (22) or (23). To verify that $A_x(t)$ is bounded, let r be an arbitrary positive constant. Then, on the interval $[-\tau_x, r]$, $A_x(t)$ assumes its maximum at some value t_m . If $t_m \in [-\tau_x, 0]$, then $A_x(t) \leq \max_{\theta \in [-\tau_x, 0]} A_x(\theta)$ for all $t \in [-\tau_x, r]$. Suppose that $\tau_m \in (0, r]$; then $\dot{A}_x(\tau_m) \geq 0$ and $A_x(t_m) \geq A_x(t_m - \tau_x)$. Therefore, from (12), we obtain

$$\begin{aligned} 0 &\leq -u_x^a A_x(t_m) + \exp(-u_x^l \tau_x) B(A_x(t_m - \tau_x)) \\ &\leq -u_x^a A_x(t_m) + \exp(-u_x^l \tau_x) B(A_x(t_m)), \end{aligned}$$

since $B(\cdot)$ is increasing. It follows from (24) that $A_x(t_m) \leq A_x^{**}$ and therefore $A_x(t) \leq A_x^{**}$ for all $t \in [-\tau_x, r]$. Since r is an arbitrary positive constant, it follows that

$$A_x(t) \leq \max \left\{ \max_{\theta \in [-\tau_x, 0]} A_x(\theta), A_x^{**} \right\}, \quad \text{for all } t \geq -\tau_x,$$

which demonstrates the boundedness of $A_x(t)$. We now show that A_x^{**} is the asymptotic bound. By the fluctuation method (Spottiswoode et al., 2012), there is a sequence of times t_n such that $t_n \rightarrow \infty$, $A_x(t_n) \rightarrow \bar{A}_x = \limsup_{t \rightarrow \infty} A_x(t)$, and $\dot{A}_x(t_n) \rightarrow 0$ as $n \rightarrow \infty$. From (12), it follows that

$$\dot{A}_x(t_n) \leq -u_x^a A_x(t_n) + \exp(-u_x^l \tau_x) B(A_x(t_n - \tau_x)).$$

Letting $n \rightarrow \infty$, applying standard property of the limsup, and the assumption that $B(\cdot)$ is increasing, we obtain

$$0 \leq -u_x^a \bar{A}_x + \exp(-u_x^l \tau_x) B(\bar{A}_x).$$

According to assumption (24), $\limsup_{t \rightarrow \infty} A_x(t) = \bar{A}_x \leq A_x^{**}$. Next, from (11) we can show that

$$\limsup_{t \rightarrow \infty} L_x(t) \leq \frac{B(\bar{A}_x)[1 - \exp(-u_x^l \tau_x)]}{u_x^l} \leq \frac{B(A_x^{**})[1 - \exp(-u_x^l \tau_x)]}{u_x^l} = L_x^{**}.$$

Finally, we show that $L_y(t)$ and $A_y(t)$ are bounded. From (10),

$$\begin{aligned} \frac{e_1 \sigma_1 L_x(t) L_y(t)}{1 + h_1 e_1 \sigma_1 L_x(t)} &= B(A_x(t)) - \frac{dL_x(t)}{dt} - u_x^l L_x(t) - \frac{e_2 \sigma_2 L_x(t) A_z(t)}{1 + h_2 e_2 \sigma_2 L_x(t) + k_2 L_y(t)} \\ &\quad - B(A_x(t - \tau_x)) \exp \left\{ - \int_{t-\tau_x}^t \left[u_x^l + \frac{e_1 \sigma_1 L_y(\theta)}{1 + h_1 e_1 \sigma_1 L_x(\theta)} - \frac{e_2 \sigma_2 L_x(\theta) A_z(\theta)}{1 + h_2 e_2 \sigma_2 L_x(\theta) + k_2 L_y(\theta)} \right] d\theta \right\} \\ &\leq B(A_x(t)) - \frac{dL_x(t)}{dt}. \end{aligned}$$

Therefore, for any $t \geq \theta$, we have

$$\begin{aligned} \int_{\theta-\tau_y}^{\theta} \exp[-u_y^l(t-\xi)] \frac{e_1 \sigma_1 L_x(\xi) L_y(\xi)}{1 + h_1 e_1 \sigma_1 L_x(\xi)} d\xi &\leq \int_{\theta-\tau_y}^{\theta} B(A_x(\xi)) d\xi - [L_x(\theta) - L_x(\theta - \tau_y)] \\ &\leq \tau_y \sup_{\theta-\tau_y \leq \xi \leq \theta} \{B(A_x(\xi))\} + L_x(\theta - \tau_y). \end{aligned}$$

Using the integral equation (19) for $L_y(t)$, it follows that

$$L_y(t) \leq \frac{C_1}{\tau_y} \int_{t-\tau_y}^t [\tau_y \sup_{\theta-\tau_y \leq \xi \leq \theta} B(A_x(\xi)) + L_x(\theta - \tau_y)] d\theta.$$

Since $A_x(t)$ and $L_x(t)$ are bounded, $L_y(t)$ is also bounded. From the boundedness of $L_y(t)$ and the equation (27), it is easy to prove that $A_y(t)$ is bounded by using a comparison argument. By the way, it is also easy to prove that $A_z(t)$ is bounded with the boundedness of $L_x(t), L_y(t)$ by using a comparison argument.

3.2 Existence of equilibria. Biological insights can be gained from a study of the equilibria of the model. In this section, we establish the existence of equilibria of the three subsystems and the whole system.

3.2.1 Cat-Cuckoo-free equilibrium. Supposing that (24) holds, we consider the following subsys-

tem with cat-cuckoo free

$$\begin{cases} \frac{dL_x(t)}{dt} = -u_x^l L_x(t) + B(A_x(t)) - B(A_x(t - \tau_x)) \exp[-\int_{t-\tau_x}^t u_x^l d\theta], \\ \frac{dA_x(t)}{dt} = -u_x^a A_x(t) + B(A_x(t - \tau_x)) \exp[-\int_{t-\tau_x}^t u_x^l d\theta]. \end{cases} \quad (28)$$

There is an equilibrium (L_x^{**}, A_x^{**}) for system (28)(system (22) with $L_y = A_y = A_z = 0$), which we refer to as the Cat-Cuckoo-free equilibrium, where $A_x^{**} > 0$ from (24), and L_x^{**}, A_x^{**} satisfy

$$\exp(-u_x^l \tau_x) B(A_x^{**}) = u_x^a A_x^{**}, \quad L_x^{**} = \frac{B(A_x^{**}(1 - \exp(-u_x^l \tau_x)))}{u_x^l}. \quad (29)$$

3.2.2 Cat-free equilibrium. Since the cuckoo is seen as a control agent for the crow. we are particularly interested in the possible existence of an equilibrium in which all four components are positive but the crow chicks and adults are present only in smaller numbers. So we consider the following crow-cuckoo subsystem

$$\begin{cases} \frac{dL_x(t)}{dt} = -u_x^l L_x(t) - \frac{e_1 \sigma_1 L_x(t) L_y(t)}{1 + h_1 e_1 \sigma_1 L_x(t)} + B(A_x(t)) \\ \quad - B(A_x(t - \tau_x)) \exp\left\{-\int_{t-\tau_x}^t \left[u_x^l + \frac{e_1 \sigma_1 L_y(\theta)}{1 + h_1 e_1 \sigma_1 L_x(\theta)}\right] d\theta\right\}, \\ \frac{dA_x(t)}{dt} = -u_x^a A_x(t) + B(A_x(t - \tau_x)) \exp\left\{-\int_{t-\tau_x}^t \left[u_x^l + \frac{e_1 \sigma_1 L_y(\theta)}{1 + h_1 e_1 \sigma_1 L_x(\theta)}\right] d\theta\right\}, \\ \frac{dL_y(t)}{dt} = -u_y^l L_y(t) + \frac{C_1}{\tau_y} \int_{t-\tau_y}^t \exp[-u_y^l(t - \xi)] \frac{e_1 \sigma_1 L_x(\xi) L_y(\xi)}{1 + h_1 e_1 \sigma_1 L_x(\xi)} d\xi \\ \quad - \frac{C_1}{\tau_y} \int_{t-2\tau_y}^{t-\tau_y} \exp[-u_y^l(t - \xi)] \frac{e_1 \sigma_1 L_x(\xi) L_y(\xi)}{1 + h_1 e_1 \sigma_1 L_x(\xi)} d\xi, \\ \frac{dA_y(t)}{dt} = -u_y^a A_y(t) + \frac{C_1}{\tau_y} \int_{t-2\tau_y}^{t-\tau_y} \exp[-u_y^l(t - \xi)] \frac{e_1 \sigma_1 L_x(\xi) L_y(\xi)}{1 + h_1 e_1 \sigma_1 L_x(\xi)} d\xi. \end{cases} \quad (30)$$

Equation (18) shows that, in such an equilibrium $(L_x^*, A_x^*, L_y^*, A_y^*, 0)$ with $L_y^* > 0$, we can have

$$L_x^* = \frac{\tau_y (u_y^l)^2}{C_1 e_1 \sigma_1 [1 - \exp(-u_y^l \tau_y)]^2 - h_1 e_1 \sigma_1 \tau_y (u_y^l)^2}. \quad (31)$$

From (31), we can obtain

$$C_1 [1 - \exp(-u_y^l \tau_y)]^2 > h_1 \tau_y (u_y^l)^2. \quad (32)$$

Remark 3.2. In fact, expression (32) is never singular, because, as we shall show, a stronger condition on C_1 is necessary for the existence of an equilibrium that is cat free. This is the condition (36), which also characterized later as one of the conditions for the persistence of the cuckoos. With L_x^* given by (31),

the L_y^* and A_x^* components of the equilibrium with the cats free are found by simultaneously solving

$$L_x^* = \frac{B(A_x^*)}{u_x^l + \frac{e_1 \sigma_1 L_y^*}{1 + h_1 e_1 \sigma_1 L_x^*}} \left\{ 1 - \exp\left[-\tau_x \left(u_x^l + \frac{e_1 \sigma_1 L_y^*}{1 + h_1 e_1 \sigma_1 L_x^*}\right)\right] \right\} \quad (33)$$

and

$$u_x^a A_x^* = B(A_x^*) \exp\left[-\tau_x \left(u_x^l + \frac{e_1 \sigma_1 L_y^*}{1 + h_1 e_1 \sigma_1 L_x^*}\right)\right]. \quad (34)$$

The following result deals with the existence of $L_y^* > 0$ and $A_x^* > 0$ satisfying (33) and (34). Later, we obtain more explicit expressions for the equilibrium components in the case when C_1 is very large.

Theorem 3.2. *If assumption (24) holds, and*

$$\frac{C_1 e_1 \sigma_1 L_x^{**}}{\tau_y (1 + h_1 e_1 \sigma_1 L_x^{**})} [1 - \exp(-u_y^l \tau_y)]^2 > (u_y^l)^2, \quad (35)$$

then system (30) has an equilibrium in which the crows and cuckoos coexist.

Proof. Each of (33) and (34) defines a curve in the (L_y^*, A_x^*) plane (recall that L_x^* is fixed and given by (31)). We rewrite (33) in the form $A_x^* = \varphi_1(L_y^*)$, where

$$\varphi_1(b) = B^{-1} \left(\frac{L_x^*}{\tau_x k \left(\tau_x \left(u_x^l + \frac{e_1 \sigma_1 b}{1 + h_1 e_1 \sigma_1 L_x^*} \right) \right)} \right)$$

with $k(b) = [(1 - \exp(-b))/b]$. Now, when $x > 0$, $k(b)$ is decreasing in b and $B^{-1}(\cdot)$ is increasing, since $B(\cdot)$ is. Thus, $\varphi_1(b)$ is increasing.

Then consider the curve defined by (34). For a particular L_y^* , let the function $\varphi_2(L_y^*)$ be defined as the solution A_x^* of (34) so that (34) is rewritten as $A_x^* = \varphi_2(L_y^*)$. Using (24) it is not difficult to see that the function $\varphi_2(b)$ is decreasing, because, if we increase the value of L_y^* , we decrease the coefficient value of the function $B(\cdot)$ in (34). The value A_x^* at which the curves $A \rightarrow u_x^a A$ and $A \rightarrow B(A) \exp[-\tau_x (u_x^l + \frac{e_1 \sigma_1 L_y^*}{1 + h_1 e_1 \sigma_1 L_x^*})]$ intersect must therefore decrease as we increase L_y^* . Moreover, this value must reach zero at a finite value of L_y^* .

According to these facts about the curves $A_x^* = \varphi_1(L_y^*)$ and $A_x^* = \varphi_2(L_y^*)$ in the (L_y^*, A_x^*) plane, it follows immediately that if $\varphi_1(0) < \varphi_2(0)$, then there exists $L_y^* > 0$ and $A_x^* > 0$ satisfying (33) and (34). Now

$$\varphi_1(0) = B^{-1} \left(\frac{L_x^*}{\tau_x k(\tau_x u_x^l)} \right) = B^{-1} \left(\frac{u_x^l L_x^*}{1 - \exp(-u_x^l \tau_x)} \right),$$

while $\varphi_2(0) = A_x^*$. Thus, the condition $\varphi_1(0) < \varphi_2(0)$ becomes

$$B(A_x^{**}) > \frac{u_x^l L_x^*}{1 - \exp(-u_x^l \tau_x)}.$$

This can be shown to be equivalent to (35), using (31) and the expression for L_x^{**} in (29).

Remark 3.3. The proof of Theorem 3.2 also implies that the coexistence equilibrium $(L_x^*, A_x^*, L_y^*, L_y^*)$ is unique. Moreover, $L_x^* < L_x^{**}$ and $A_x^* < A_x^{**}$ if the coexistence equilibrium exists.

If the assumptions of Theorem 3.2 hold, further useful insights can be obtained by supposing that the parameter values are such that the equilibrium L_x^* is low, i.e., expression (31) is low. For example, we might assume that the conversion efficiency C_1 is large. Then we also expect the equilibrium A_x^* to be on the low side so that $B(A_x^*) \approx \dot{B}(0)A_x^*$. From (34), we then obtain an explicit expression for L_y^* :

$$L_y^* = \frac{1 + h_1 e_1 \sigma_1 L_x^*}{e_1 \sigma_1} \left[\frac{1}{\tau_x} \ln\left(\frac{\dot{B}(0)}{u_x^a}\right) - u_x^l \right] \quad (36)$$

with L_x^* given by (31). Then, from (33),

$$A_x^* = \frac{L_x^* \ln(\dot{B}(0)/u_x^a)}{\dot{B}(0)\tau_x(1 - u_x^a/\dot{B}(0))}. \quad (37)$$

Expression (37) is automatically positive, while (36) is positive because of (25).

From (20), A_y^* is given in terms of other equilibrium components by

$$A_y^* = \frac{C_1 e_1 \sigma_1 \exp(-u_y^l \tau_y) [1 - \exp(-u_y^l \tau_y)] L_x^* L_y^*}{u_y^l u_y^a \tau_y (1 + h_1 e_1 \sigma_1 L_x^*)} \quad (38)$$

without further parameter restrictions. We conclude that, if the numbers of crow chicks and adults are small (for example, if C_1 is very large), then the equilibrium which is free of cats is given approximately by (31), (36), (37) and (38).

3.2.3 Cuckoo-free equilibrium. Since the cat is seen as a predator for the crow chicks, we are particularly interested in the possible existence of an equilibrium $(L_x^{***}, A_x^{***}, A_z^{***})$. Then we consider the following crow-cat subsystem

$$\begin{cases} \frac{dL_x(t)}{dt} = -u_x^l L_x(t) - \frac{e_2 \sigma_2 L_x(t) A_z(t)}{1 + h_2 e_2 \sigma_2 L_x(t)} + B(A_x(t)) \\ \quad - B(A_x(t - \tau_x)) \exp\left\{ - \int_{t-\tau_x}^t \left[u_x^l + \frac{e_2 \sigma_2 A_z(\theta)}{1 + h_2 e_2 \sigma_2 L_x(\theta)} \right] d\theta \right\}, \\ \frac{dA_x(t)}{dt} = -u_x^a A_x(t) + B(A_x(t - \tau_x)) \exp\left\{ - \int_{t-\tau_x}^t \left[u_x^l + \frac{e_2 \sigma_2 A_z(\theta)}{1 + h_2 e_2 \sigma_2 L_x(\theta)} \right] d\theta \right\}, \\ \frac{dA_z(t)}{dt} = -u_z^a A_z(t) + \frac{C_2 e_2 \sigma_2 L_x(t) A_z(t)}{1 + h_2 e_2 \sigma_2 L_x(t)}. \end{cases} \quad (39)$$

From (21), we obtain

$$L_x^{***} = \frac{u_z^a (1 + h_2 e_2 \sigma_2)}{C_2 e_2 \sigma_2}. \quad (40)$$

Obviously, (40) is positive because all parameters are positive constants. With L_x^{***} given by (40), the A_x^{***} and A_z^{***} components of an equilibrium with the cat present are found by simultaneously solving

$$L_x^{***} = B(A_x^{***}) \frac{1}{u_x^l + \frac{e_2 \sigma_2 A_z^{***}}{1 + h_2 e_2 \sigma_2 A_z^{***}}} \left\{ 1 - \exp\left[-\tau_x \left(u_x^l + \frac{e_2 \sigma_2 A_z^{***}}{1 + h_2 e_2 \sigma_2 L_x^{***}} \right) \right] \right\} \quad (41)$$

and

$$u_x^a A_x^{***} = B(A_x^{***}) \exp\left[-\tau_x \left(u_x^l + \frac{e_2 \sigma_2 A_z^{***}}{1 + h_2 e_2 \sigma_2 L_x^{***}}\right)\right]. \quad (42)$$

Later, we obtain a more explicit expression for the equilibrium components in the case when C_2 is very large.

Theorem 3.3. *If assumption (24) holds, and*

$$C_2 e_2 \sigma_2 L_x^{**} [1 - \exp(-u_x^l \tau_x)] > u_z^a (1 + h_2 e_2 \sigma_2), \quad (43)$$

then system (39) has an equilibrium in which the crow and cat coexist.

Proof. Each of (41) and (42) defines a curve in the (A_z^{***}, A_x^{***}) plane (recall that L_x^{***} is fixed and given by (40)). We can write (41) in the form $A_x^{***} = \varphi_3(A_z^{***})$, where

$$\varphi_3(b) = B^{-1}\left(\frac{L_x^{***}}{\tau_x k\left(\tau_x \left(u_x^l + \frac{e_2 \sigma_2 b}{1 + h_2 e_2 \sigma_2 L_x^{***}}\right)\right)}\right)$$

with $k(b) = [(1 - \exp(-b))/b]$. Now, when $x > 0$, $k(b)$ is decreasing in b and $B^{-1}(\cdot)$ is increasing, since $B(\cdot)$ is. Thus, $\varphi_3(b)$ is increasing.

Now consider the curve defined by (42). For a particular A_z^{***} , let the function $\varphi_4(A_z^{***})$ be defined as the solution A_x^{***} of (42) so that (42) is rewritten as $A_x^{***} = \varphi_4(A_z^{***})$. It is easy to see, using (24), that the function $\varphi_4(b)$ is thus defined is decreasing, because, if we increase the value of A_z^{***} , the coefficient value of the function $B(\cdot)$ in (42) decreases. The value A_x^{***} at which the curves $A \rightarrow u_x^a A$ and $A \rightarrow B(A) \exp[-\tau_x (u_x^l + \frac{e_2 \sigma_2 A_z^{***}}{1 + h_2 e_2 \sigma_2 L_x^{***}})]$ intersect must therefore decrease as we increase A_z^{***} . Moreover, this value must reach zero at a finite value of A_z^{***} .

In view of these facts about the curves $A_x^{***} = \varphi_3(A_z^{***})$ and $A_x^{***} = \varphi_4(A_z^{***})$ in the (A_x^{***}, A_z^{***}) plane, it follows immediately that, there exists $A_x^{***} > 0$ and $A_z^{***} > 0$ satisfying (41) and (42) when $\varphi_3(0) < \varphi_4(0)$. Now

$$\varphi_3(0) = B^{-1}\left(\frac{L_x^{***}}{\tau_x k(\tau_x u_x^l)}\right) = B^{-1}\left(\frac{u_x^l L_x^{***}}{1 - \exp(-u_x^l \tau_x)}\right),$$

while $\varphi_4(0) = A_x^{**}$. Thus, the condition $\varphi_3(0) < \varphi_4(0)$ becomes

$$B(A_x^{**}) > \frac{u_x^l L_x^{***}}{1 - \exp(-u_x^l \tau_x)}.$$

Then taking (40) into the above expression, we can obtain

$$C_2 e_2 \sigma_2 L_x^{**} [1 - \exp(-u_x^l \tau_x)] > u_z^a (1 + h_2 e_2 \sigma_2).$$

This can be shown to be equivalent to (43).

Remark 3.4. The proof of Theorem 3.3 also implies that the coexistence equilibrium $(L_x^{***}, A_x^{***}, A_z^{***})$ is unique. Moreover, $L_x^{***} < L_x^{**}$ and $A_x^{***} < A_x^{**}$ if the coexistence equilibrium exists.

If the assumptions of Theorem 3.3 hold, further useful insights can be gained by supposing the

parameter values are such that the equilibrium L_x^{***} is low, i.e., expression (40) is low. For example, we might assume that the conversion efficiency C_2 is large. Then, we also expect the equilibrium A_x^{***} to be on the low side such that $B(A_x^{***}) \approx \dot{B}(0)A_x^{***}$. From (42), we then obtain an explicit expression for A_z^{***} :

$$A_z^{***} = \frac{1 + h_2 e_2 \sigma_2 L_x^{***}}{e_2 \sigma_2} \left[\frac{1}{\tau_x} \ln\left(\frac{\dot{B}(0)}{u_x^a}\right) - u_x^l \right] \quad (44)$$

with L_x^{***} given by (40). Then, from (41),

$$A_x^{***} = \frac{L_x^{***} \ln(\dot{B}(0)/u_x^a)}{\dot{B}(0)\tau_x(1 - u_x^a/\dot{B}(0))}. \quad (45)$$

Expression (45) is surely positive, while (44) is positive because of (25).

We conclude that if the populations of crows chicks and adults are small (for example, if C_2 is very large), then the equilibrium in which the cats are free is given approximately by (40), (44) and (45).

3.2.4 Crow-Cuckoo-Cat coexistence equilibrium. The study of the whole system is very significant in this paper. So it is important to consider the existence of the Crow-Cuckoo-Cat coexistence equilibrium $(\tilde{L}_x, \tilde{A}_x, \tilde{L}_y, \tilde{A}_y, \tilde{A}_z)$. From the equation (18), we can get

$$\tilde{L}_x = \frac{\tau_y (u_y^l)^2}{C_1 e_1 \sigma_1 [1 - \exp(-u_y^l \tau_y)]^2 - h_1 e_1 \sigma_1 \tau_y (u_y^l)^2}. \quad (46)$$

Observe that, necessarily,

$$C_1 e_1 \sigma_1 [1 - \exp(-u_y^l \tau_y)]^2 > h_1 e_1 \sigma_1 \tau_y (u_y^l)^2. \quad (47)$$

Expression (46) is never singular in practice, because a stronger condition C_1 is in fact necessary for the existence of an equilibrium with the cuckoo present. Then with the \tilde{L}_x given by (46), from (21), we can get that

$$\tilde{L}_y = \frac{C_2 e_2 \sigma_2 \tilde{L}_x - u_z^a h_2 e_2 \sigma_2 \tilde{L}_x - u_z^a}{u_z^a k_2}. \quad (48)$$

Observe that, necessarily,

$$C_2 e_2 \sigma_2 \tilde{L}_x - u_z^a h_2 e_2 \sigma_2 \tilde{L}_x - u_z^a > 0. \quad (49)$$

Taking (46) into (49) and combining (47), we finally get

$$(C_2 e_2 \sigma_2 - u_z^a h_2 e_2) \tau_y (u_y^l)^2 - u_z^a C_1 e_1 \sigma_1 [1 - \exp(-u_y^l \tau_y)]^2 + u_z^a h_1 e_1 \sigma_1 \tau_y (u_y^l)^2 > 0.$$

With the \tilde{L}_x, \tilde{L}_y given by (46) and (49), the \tilde{A}_x and \tilde{A}_z components of an equilibrium are found by simultaneously solving

$$\begin{aligned} \tilde{L}_x = B(\tilde{A}_x) & \frac{1}{u_x^l + \frac{e_1 \sigma_1 \tilde{L}_y}{1 + h_1 e_1 \sigma_1 \tilde{L}_x} + \frac{e_2 \sigma_2 \tilde{A}_z}{1 + h_2 e_2 \sigma_2 \tilde{L}_x + k_2 \tilde{L}_y}} \\ & \left\{ 1 - \exp \left[- \left(u_x^l + \frac{e_1 \sigma_1 \tilde{L}_y}{1 + h_1 e_1 \sigma_1 \tilde{L}_x} + \frac{e_2 \sigma_2 \tilde{A}_z}{1 + h_2 e_2 \sigma_2 \tilde{L}_x + k_2 \tilde{L}_y} \right) \tau_x \right] \right\} \end{aligned} \quad (50)$$

and

$$u_x^a \tilde{A}_x = B(\tilde{A}_x) \exp \left[- \left(u_x^l + \frac{e_1 \sigma_1 \tilde{L}_y}{1 + h_1 e_1 \sigma_1 \tilde{L}_x} + \frac{e_2 \sigma_2 \tilde{A}_z}{1 + h_2 e_2 \sigma_2 \tilde{L}_x + k_2 \tilde{L}_y} \right) \tau_x \right]. \quad (51)$$

The following results deal with the existence of $\tilde{A}_z > 0$ and $\tilde{A}_x > 0$ satisfying (50) and (51).

Theorem 3.4. *If assumption (24) holds, and*

$$B \left(\frac{B(\tilde{A}_x) \exp[-(u_x^l + \frac{e_1 \sigma_1 \tilde{L}_y}{1 + h_1 e_1 \sigma_1 \tilde{L}_x}) \tau_x]}{u_x^a} \right) > \frac{\tilde{L}_x (u_y^l + \frac{e_1 \sigma_1 \tilde{L}_y}{1 + h_1 e_1 \sigma_1 \tilde{L}_x})}{1 - \exp[-(u_x^l + \frac{e_1 \sigma_1 \tilde{L}_y}{1 + h_1 e_1 \sigma_1 \tilde{L}_x}) \tau_x]}, \quad (52)$$

then system (22) or (23) has an equilibrium in which the crows, cuckoos and cats coexist.

Proof. Each of (50) and (51) defines a curve in the $(\tilde{A}_z, \tilde{A}_x)$ plane (recall that \tilde{L}_x and \tilde{L}_y is fixed and given by (46) and (48)). We rewrite (50) in the form $\tilde{A}_x = \varphi_5(\tilde{A}_z)$, where

$$\varphi_5(b) = B^{-1} \left(\frac{\tilde{L}_x}{\tau_x k \left(\tau_x (u_x^l + \frac{e_1 \sigma_1 \tilde{L}_y}{1 + h_1 e_1 \sigma_1 \tilde{L}_x} + \frac{e_2 \sigma_2 b}{1 + h_2 e_2 \sigma_2 \tilde{L}_x + k_2 \tilde{L}_y}) \right)} \right)$$

with $k(b) = [(1 - \exp(-b))/b]$. Now, when $x > 0$, then $k(b)$ is decreasing in b and $B^{-1}(\cdot)$ is increasing, since $B(\cdot)$ is. Thus, $\varphi_5(b)$ is increasing.

Now consider the curve defined by (51). For a particular \tilde{A}_z , let the function $\varphi_6(\tilde{A}_z)$ be defined as the solution \tilde{A}_x of (51) so that (51) is rewritten as $\tilde{A}_x = \varphi_6(\tilde{A}_z)$. It is easy to see, using (24), that the function $\varphi_6(b)$ thus defined is decreasing, because the coefficient of the function $B(\cdot)$ in (51) decrease as the value of \tilde{A}_z increases. The value \tilde{A}_x at which the curves $A \rightarrow u_x^a A$ and $A \rightarrow B(A) \exp[-\tau_x (u_x^l + \frac{e_1 \sigma_1 \tilde{L}_y}{1 + h_1 e_1 \sigma_1 \tilde{L}_x} + \frac{e_2 \sigma_2 \tilde{A}_z}{1 + h_2 e_2 \sigma_2 \tilde{L}_x + k_2 \tilde{L}_y})]$ intersect must therefore decrease as we increase \tilde{A}_z . Moreover, this value must reach zero at a finite value of \tilde{A}_z .

In view of these facts about the curves $\tilde{A}_x = \varphi_5(\tilde{A}_z)$ and $\tilde{A}_x = \varphi_6(\tilde{A}_z)$ in the $(\tilde{A}_x, \tilde{A}_z)$ plane, it follows immediately that, if $\varphi_5(0) < \varphi_6(0)$, then there exist $\tilde{A}_x > 0$ and $\tilde{A}_z > 0$ satisfying (50) and (51). Now

$$\varphi_5(0) = B^{-1} \left(\frac{\tilde{L}_x (u_x^l + \frac{e_1 \sigma_1 \tilde{L}_y}{1 + h_1 e_1 \sigma_1 \tilde{L}_x})}{1 - \exp[-(u_x^l + \frac{e_1 \sigma_1 \tilde{L}_y}{1 + h_1 e_1 \sigma_1 \tilde{L}_x}) \tau_x]} \right),$$

while

$$\varphi_6(0) = \frac{B(\tilde{A}_x) \exp[-u_x^l + \frac{e_1 \sigma_1 \tilde{L}_y}{1 + h_1 e_1 \sigma_1 \tilde{L}_x} \tau_x]}{u_x^a}.$$

Thus, the condition $\varphi_5(0) < \varphi_6(0)$ becomes the condition (52).

4 Main results

4.1 Global stability of the Cuckoo-Cat-free equilibrium

The following theorem shows that if the biomass conversion efficiencies C_1, C_2 are low enough or

the cats and the cuckoo nestlings take much time to digest their food (h_1, h_2 are very large), then the cuckoo-cat pair will be driven to extinction.

Theorem 4.1. *Suppose that*

$$\frac{C_1 e_1 \sigma_1}{\tau_y (1 + h_1 e_1 \sigma_1 L_x^{**})} [1 - \exp(-u_y^l \tau_y)]^2 < (u_y^l)^2 \quad (53)$$

and

$$\frac{C_2 e_2 \sigma_2 L_x^{**}}{1 + h_2 e_2 \sigma_2 L_x^{**}} < u_z^a, \quad (54)$$

then the Cuckoo-Cat-free equilibrium $(L_x^{**}, A_x^{**}, 0, 0, 0)$ of system (28) is globally asymptotically stable for all nonnegative solutions with $A_x(\theta) \neq 0$ on $[-\tau_x, 0]$.

Proof. We use the variant of the model that involves the integral equations (11) and (19). From (12) and the positivity of solutions, we have

$$\frac{dA_x(t)}{dt} \leq -u_x^a A_x(t) + B(A_x(t - \tau_x)) \exp(-u_x^l \tau_x). \quad (55)$$

Since $B(\cdot)$ is increasing, we may use a comparison argument (for example see Smith, 1995) to conclude that $A_x(t)$ is bounded by the solution of the corresponding differential equation obtained from (55) by changing. Since $B(\cdot)$ is increasing, positive solution of that differential equation approaches A_x^{**} (see Kuang, 1993). Therefore,

$$\limsup_{t \rightarrow \infty} A_x(t) \leq A_x^{**},$$

and from (29) we have

$$\limsup_{t \rightarrow \infty} L_x(t) \leq \frac{B(A_x^{**}) [1 - \exp(-u_x^l \tau_x)]}{u_x^l} = L_x^{**}.$$

Since (53) holds, there exists a small enough positive constant ϵ such that

$$(u_y^l)^2 > \frac{C_1 e_1 \sigma_1 (L_x^{**} + \epsilon)}{\tau_y (1 + h_1 e_1 \sigma_1 (L_x^{**} + \epsilon))} [1 - \exp(-u_y^l \tau_y)]^2. \quad (56)$$

With this ϵ , $L_x \leq L_x^{**} + \epsilon$ for t sufficiently large. From (19) and for t sufficiently large, we obtain

$$L_y(t) \leq \frac{C_1}{\tau_y} \int_{t-\tau_y}^t \int_{\theta-\tau_y}^{\theta} \exp[-u_y^l (t - \xi)] \frac{e_1 \sigma_1 (L_x^{**} + \epsilon) L_y(\xi)}{1 + h_1 e_1 \sigma_1 (L_x^{**} + \epsilon)} d\xi d\theta, \quad (57)$$

because the integrand of (18) increases with respect to $L_x(\xi)$. Any solution of inequality (57) is bounded above by the solution $\check{L}_y(t)$ of the corresponding integral equation

$$\check{L}_y(t) \leq \frac{C_1}{\tau_y} \int_{t-\tau_y}^t \int_{\theta-\tau_y}^{\theta} \exp[-u_y^l (t - \xi)] \frac{e_1 \sigma_1 (L_x^{**} + \epsilon) \check{L}_y(\xi)}{1 + h_1 e_1 \sigma_1 (L_x^{**} + \epsilon)} d\xi d\theta, \quad (58)$$

such that $\check{L}_y(\theta) \geq L_y(\theta)$ for all $\theta \in [-2\tau_y, 0]$. Indeed, it is straightforward to show, since (58) is linear and has a positive kernel, that the variable $\check{L}_y(\theta_0) - L_y(t)$ can never become negative. Actually, (57) holds

only for t sufficiently large, but the comparison argument still holds for a suitable solution $\check{L}_y(t)$ of (58). In fact, the solution map of (58) is strongly positive: if $L_y(\theta) \geq 0$ for all $\theta \in [-2\tau, 0]$ and $\check{L}_y(\theta_0) > 0$ for some $\theta_0 \in [-2\tau, 0]$, then $\check{L}_y(t) > 0$ for all $t > 2\tau$. Moreover, since (58) has a positive kernel, by the Krein-Rutman theorem it suffices to consider only the real roots of the characteristic equation that results from a search for solutions of the form $\check{L}_y(t) = \exp(\lambda t)$. Inserting it into (18), we can get

$$(\lambda + u_y^l)^2 = \frac{C_1 e_1 \sigma_1 (L_x^{**} + \epsilon)}{\tau_y (1 + h_1 e_1 \sigma_1 (L_x^{**} + \epsilon))} [1 - \exp(-u_y^l \tau_y)]^2. \quad (59)$$

In view of all these facts, to show that $\check{L}_y(t) \rightarrow 0$ (and hence $L_y(t) \rightarrow 0$) as $t \rightarrow \infty$, it suffices to prove that all the real roots of (59) are negative. Note that, since (56) holds, the left-hand side of (59) exceeds its right-hand side when $\lambda = 0$. To simplify the notation, we denote

$$M = \frac{C_1 e_1 \sigma_1 (L_x^{**} + \epsilon)}{\tau_y [1 + h_1 e_1 \sigma_1 (L_x^{**} + \epsilon)]}.$$

Then we have $M[1 - \exp(-u_y^l \tau_y)]^2 \leq (u_y^l)^2$. The real roots of (59) must satisfy one of the following equations:

$$m(\lambda) := \sqrt{M} \{1 - \exp[-(\lambda + u_y^l) \tau_y]\} + (\lambda + u_y^l) = 0,$$

$$n(\lambda) := \sqrt{M} \{1 - \exp[-(\lambda + u_y^l) \tau_y]\} - (\lambda + u_y^l) = 0.$$

The function $y = m(\lambda)$ satisfies $\lim_{\lambda \rightarrow -\infty} m(\lambda) = -\infty$, $\lim_{\lambda \rightarrow +\infty} m(\lambda) = +\infty$, and $\dot{m}(\lambda) > 0$. Moreover, $m(0) = \sqrt{M}[1 - \exp(-u_y^l \tau_y)] + u_y^l \geq 0$. Therefore, the equation $m(\lambda) = 0$ has just one real root and it is negative.

The function $y = n(\lambda)$ satisfies $\lim_{\lambda \rightarrow -\infty} n(\lambda) = -\infty$, $\lim_{\lambda \rightarrow +\infty} n(\lambda) = -\infty$. Moreover, $\dot{n}(\lambda) = \sqrt{M} \tau_y \exp[-(\lambda + u_y^l) \tau_y] - 1$. If we let $\dot{n}(\lambda_0) = 0$, then $\sqrt{M} \tau_y \exp[-(\lambda_0 + u_y^l) \tau_y] = 1$ and $\lambda_0 = \frac{\ln(\tau_y \sqrt{M})}{\tau_y} - u_y^l$. It is easy to see that $\dot{n}(\lambda) > 0$ if $\lambda < \lambda_0$ and $\dot{n}(\lambda) < 0$ if $\lambda > \lambda_0$. Since $n(0) = \sqrt{M}[1 - \exp(-u_y^l \tau_y)] - u_y^l \leq 0$, to show that the equation $n(\lambda) = 0$ has no positive real roots, it suffices to prove that $\dot{n}(0) \leq 0$. In fact, since $M[1 - \exp(-u_y^l \tau_y)]^2 < (u_y^l)^2$, we have

$$\sqrt{M} < \frac{u_y^l}{1 - \exp(-u_y^l \tau_y)}.$$

Therefore,

$$\begin{aligned} \dot{n}(0) &= \sqrt{M} \tau_y \exp(-u_y^l \tau_y) - 1 \\ &< \frac{u_y^l}{1 - \exp(-u_y^l \tau_y)} \tau_y \exp(-u_y^l \tau_y) - 1 \\ &= \frac{1}{1 - \exp(-u_y^l \tau_y)} \{u_y^l \tau_y \exp(-u_y^l \tau_y) - [1 - \exp(-u_y^l \tau_y)]\}. \end{aligned}$$

Define $H(u) := u \exp(-u) - 1 + \exp(-u)$. It is easy to show that $H(u) < 0$ for $u > 0$, and therefore $\dot{n}(0) < 0$. Hence, the equation $n(\lambda) = 0$ has no real positive roots. Therefore, all real roots of (59) are negative, and hence $L_y(t) \rightarrow 0$ as $t \rightarrow \infty$. From (20), it follows that $A_y(t) \rightarrow 0$. Finally, from (21), we

obtain that

$$A_z(t) = A_z(0) \exp \left[\int_0^t \left(-u_z^a + \frac{C_2 e_2 \sigma_2 L_x(s)}{1 + h_2 e_2 \sigma_2 L_x(s) + k_2 L_y(s)} \right) ds \right]$$

Hence, $A_z(t) \rightarrow 0$ as $t \rightarrow \infty$ because of the condition (54). At the same time, the equation (12) can be considered as an asymptotically autonomous equation, with the following equation:

$$\frac{dA_x(t)}{dt} = -u_x^a A_x(t) + B(A_x(t - \tau_x)) \exp(-u_x^l \tau_x),$$

the solution $A_x(t)$ of which tend to A_x^{**} , as noted earlier in this proof, since $A_x(\theta) \neq 0$ on $[-\tau_x, 0]$. This argument can be justified using established theories on asymptotically autonomous systems (e.g. Thieme, 1992; Mischaikow et al., 1995). Finally, the limit of the integral equation (11) when $t \rightarrow \infty$, shows that

$$L_x(t) \rightarrow L_x^{**}.$$

This completes the proof of Theorem 4.1.

4.2 The mutualism of the Crows and Cuckoos with the Cats free

In this subsection, we show that under condition (60), the cuckoo population uniformly and strongly persists. Uniform strong persistence of the cuckoos implies that the cuckoos do not go extinct and also that, except for initial transients, its population will always be above some minimum threshold that does not depend on the initial values. Moreover, the cuckoos and crows will be in a mutualistic state free of cats.

Theorem 4.2. *Suppose that (24) holds and that*

$$\frac{C_1 e_1 \sigma_1}{\tau_y (1 + h_1 e_1 \sigma_1 L_x^{**})} [1 - \exp(-u_y^l \tau_y)]^2 > (u_y^l)^2 \quad (60)$$

with L_x^{**} given in (26). Then the cuckoos and crows uniformly persist in the sense that there exists a small enough $\eta > 0$ such that

$$\liminf_{t \rightarrow \infty} x_i(t) > \eta, \quad i = 1, 2, 3, 4,$$

for all solutions $x(t) = (L_x, A_x, L_y, A_y)$ of the system (30) with $A_x(\theta) \neq 0, \theta \in [-\tau_x, 0]$.

Proof. Denote

$$\begin{aligned} \tau &= \max\{\tau_x, 2\tau_y\}, & M &:= C([- \tau, 0], \mathbb{R}_+^4), \\ \chi(\theta) &= (L_x(\theta), A_x(\theta), L_y(\theta), A_y(\theta)), & \theta &\in [- \tau, 0], \end{aligned} \quad (61)$$

$$M_0 := \{\chi \in M : \chi_i(0) > 0, i = 1, 2, 3, 4\} \quad \text{and} \quad \partial M_0 := M \setminus M_0.$$

Clearly, M_0 is an open set relative to M . Define the solution semiflow $\psi(t)$ by

$$\psi(t)\chi(\theta) = (L_x(t + \theta), A_x(t + \theta), L_y(t + \theta), A_y(t + \theta)) = \psi(t + \theta),$$

where $(L_x(t), A_x(t), L_y(t), A_y(t))$ is the solution of the system (30) with initial value (61). It then follows from Theorem 3.1 that $\psi(t)$ is point dissipative and $\chi(t)M_0 \in M_0$. Let $\omega(\chi)$ be the ω -limit set of the

orbit

$$\gamma^+(\chi) := \{\psi(t)\chi : \text{for all } t \geq 0\},$$

and define

$$M_\partial := \{\chi \in \partial M_0 : \psi(t)\chi \in \partial M_0, t \geq 0\}.$$

In view of the proof of Theorem 3.1, we have

$$\omega(\chi) = \{(0, 0, 0, 0), (L_x^{**}, A_x^{**}, 0, 0)\} \quad \text{for all } \chi \in M_\partial.$$

Now, we prove the claim : there exists $\epsilon > 0$ such that for all solution (L_x, A_x, L_y, A_y) with $A_x(\theta) \neq 0$ on $[-\tau_x, 0]$, we have

$$\limsup_{t \rightarrow \infty} L_y(t) \geq \epsilon.$$

Suppose the claim is not true, then for any $\epsilon > 0$ there exists a solution $L_y(t)$ with

$$\bar{L}_y < \epsilon, \tag{62}$$

where the $\bar{L}_y = \limsup_{t \rightarrow \infty} L_y(t)$. Later, we shall choose an ϵ that produces a contradiction. Because the inequality (62) holds, $L_y < \epsilon$ for all t sufficiently large. Because the integrand of the integral term in (20) increases with $L_x(\xi)$, from that equation we obtain

$$\begin{aligned} \frac{dA_y(t)}{dt} &\leq -u_y^a A_y(t) + \frac{C_1 \epsilon}{h_1 \tau_y} \int_{t-2\tau_y}^{t-\tau_y} \exp[-u_y^l(t-\xi)] d\xi \\ &\leq -u_y^a A_y(t) + \frac{C_1 \epsilon}{h_1} \end{aligned}$$

and therefore

$$\bar{L}_y \leq \frac{C_1 \epsilon}{h_1 u_y^a}.$$

Also for t sufficiently large, by $L_y(t) < \epsilon$ and the (12), we get

$$\frac{dA_x(t)}{dt} \geq -u_x^a A_x(t) + \exp[-(u_x^l + e_1 \sigma_1 \epsilon) \tau_x] B(A_x(t - \tau_x)).$$

By assumption (24), if ϵ is sufficiently small, then there exists $A_x^{**}(\epsilon) > 0$ such that

$$\exp[-(u_x^l + e_1 \sigma_1 \epsilon) \tau_x] B(A) > u_x^a A \quad \text{when } 0 < A < A_x^{**}(\epsilon),$$

$$\exp[-(u_x^l + e_1 \sigma_1 \epsilon) \tau_x] B(A) < u_x^a A \quad \text{when } A > A_x^{**}(\epsilon).$$

Moreover, $A_x^{**}(\epsilon) \rightarrow A_x^{**}$ when $\epsilon \rightarrow 0$. Since $B(\cdot)$ is increasing, we may apply a comparison argument similar to that described in the proof of Theorem 4.1 to conclude that

$$\underline{A}_x := \liminf_{t \rightarrow \infty} A_x(t) \geq A_x^{**}(\epsilon). \tag{63}$$

For t sufficiently large, we have $L_y(t) < \epsilon$. By (63) and the monotonicity of function $B(\cdot)$, taking the limit inferior as $t \rightarrow \infty$ in the (11), we obtain

$$\underline{L}_x \geq \frac{B(A_x^{**}(\epsilon))}{u_x^l + e_1 \sigma_1 \epsilon} \exp[-(u_x^l + e_1 \sigma_1 \epsilon) \tau_x] := L_x^{**}(\epsilon). \quad (64)$$

where $\underline{L}_x = \liminf_{t \rightarrow \infty} L_x(t)$. Note that $L_x^{**}(\epsilon) \rightarrow L_x^{**}$ as $\epsilon \rightarrow 0$. From (64), $L_x(t) \geq L_x^{**}(\epsilon) - \epsilon$ for t sufficiently large. Because the integrand of (19) increases with $L_x(\xi)$, we obtain from that inequality

$$L_y(t) \geq \frac{C_1}{\tau_y} \int_{t-\tau_y}^t \int_{\theta-\tau_y}^{\theta} \exp[-u_y^l(t-\xi)] \frac{e_1 \sigma_1 (L_x^{**}(\epsilon) - \epsilon) L_y(\xi)}{1 + h_1 e_1 \sigma_1 (L_x^{**}(\epsilon) - \epsilon)} d\xi d\eta. \quad (65)$$

We now use another comparison argument to show that $L_y(t)$ grows exponentially with t , which contradicts with (62). We achieve this by a study of the characteristic equation of the integral equation (65)(changing \geq to $=$). That characteristic equation becomes

$$(u_y^l + \lambda)^2 = \frac{C_1 e_1 \sigma_1 (L_x^{**}(\epsilon) - \epsilon)}{\tau_y (1 + h_1 e_1 \sigma_1 (L_x^{**}(\epsilon) - \epsilon))} \{1 - \exp[-(\lambda + u_y^l) \tau_y]\}^2. \quad (66)$$

Then we choose a small enough positive constant ϵ such that

$$(u_y^l)^2 < \frac{C_1 e_1 \sigma_1 (L_x^{**}(\epsilon) - \epsilon)}{\tau_y (1 + h_1 e_1 \sigma_1 (L_x^{**}(\epsilon) - \epsilon))} [1 - \exp(-u_y^l \tau_y)]^2, \quad (67)$$

which is possible because of the condition (60). Therefore, the left-hand side of (66) is less than the right-hand side when $\lambda = 0$. Since the left-hand side grows without bound with λ while the right-hand side tends to a constant, it follows that (66) has a positive real root. Therefore, $L_y(t)$ grows exponentially, which leads to a contradiction with (62).

The above claim shows that both $M_1(0, 0, 0, 0)$ and $M_2(L_x^{**}, A_y^{**}, 0, 0)$ are uniform weak repellers for M_0 in the sense that

$$\limsup_{t \rightarrow \infty} \|\psi(t)\chi - M_i\| \geq \epsilon \quad \text{for all } \chi \in M_0, i = 1, 2,$$

with the maximum norm $\|\cdot\|$. Define a continuous function $G : M \rightarrow R_+$ by

$$G(\chi) = \min(\chi_1(0), \chi_2(0), \chi_3(0), \chi_4(0)) \quad \text{for all } \chi = (\chi_1, \chi_2, \chi_3, \chi_4) \in M.$$

Thus, G is a generalized distance function for the semiflow $\psi(t)$ (Definition 1.3.1 of Zhao, 2003). It then follows from the Theorem 1.3.2 of Zhao (2003) that there exists a constant $\eta > 0$ such that $\min\{G(\varrho) : \varrho \in \omega(\chi)\} > \eta$ for any $\chi(\theta) \neq 0$ on $[-\tau_x, 0]$. Hence,

$$\liminf_{t \rightarrow \infty} L_x(t) \geq \eta, \quad \liminf_{t \rightarrow \infty} A_x(t) \geq \eta, \quad \liminf_{t \rightarrow \infty} L_y(t) \geq \eta, \quad \liminf_{t \rightarrow \infty} A_y(t) \geq \eta$$

uniformly for all solutions with $A_x(\theta) \neq 0$ on $[-\tau_x, 0]$. This completes the proof of Theorem 4.2.

4.3 The persistence of the Cat-Crow with the Cuckoos free

In this subsection, we show under condition (68) that the crows and cats are uniformly and strongly

persistent.

Theorem 4.3. *Suppose that (24) holds and*

$$\frac{C_2 e_2 \sigma_2 L_x^{**}}{1 + h_2 e_2 \sigma_2 L_x^{**}} > u_z^a \quad (68)$$

with L_x^{**} given in (26). Then the crows and cats are uniformly persistent in the sense that there exists a constant $\alpha > 0$ such that

$$\liminf_{t \rightarrow \infty} x_i(t) > \alpha, \quad i = 1, 2, 3,$$

for all solutions $x(t) = (L_x, A_x, A_z)$ of the (39) with $A_x(\theta) \neq 0, \theta \in [-\tau_x, 0]$.

Proof. Denote

$$F := C([-\tau_1, 0], \mathbb{R}_+^3),$$

$$\varphi(\theta) = (L_x(\theta), A_x(\theta), A_z(\theta)), \quad \theta \in [-\tau_1, 0], \quad (69)$$

$$F_0 := \{\varphi \in M : \varphi_i(0) > 0, i = 1, 2, 3, 4\} \quad \text{and} \quad \partial F_0 := F \setminus F_0.$$

Clearly, F_0 is an open set relative to F . Define the solution semiflow $\psi(t)$ by

$$\psi(t)\varphi(\theta) = (L_x(t + \theta), A_x(t + \theta), A_z(t + \theta)) = \psi(t + \theta),$$

where $(L_x(t), A_x(t), A_z(t))$ is the solution of the system (39) with initial value (69). It then follows from the Theorem 3.1 that $\psi(t)$ is point dissipative and $\chi(t)F_0 \in F_0$. Let $\omega(\chi)$ be the ω -limit set of the orbit

$$\gamma^+(\psi) := \{\psi(t)\varphi : \text{for all } t \geq 0\}$$

and define

$$F_\partial := \{\varphi \in \partial F_0 : \psi(t)\varphi \in \partial F_0, t \geq 0\}.$$

In view of the proof of the Theorem 3.1, we have

$$\omega(\varphi) = \{(0, 0, 0, 0), (L_x^{**}, A_x^{**}, 0)\} \quad \text{for all } \varphi \in F_\partial.$$

Now, we prove the claim : there exists a constant $\delta > 0$ such that for all solution (L_x, A_x, A_z) with $A_x(\theta) \neq 0$ on $[-\tau_x, 0]$, we have

$$\limsup_{t \rightarrow \infty} A_z(t) \geq \delta.$$

Suppose the claim is not true, then for any $\delta > 0$ there exists a solution $A_z(t)$ with

$$\bar{A}_z < \delta \quad (70)$$

where the $\bar{A}_z = \limsup_{t \rightarrow \infty} A_z(t)$. Because the inequality (70) holds, $A_z(t) < \delta$ for all t sufficiently large.

From that equation (39) we obtain

$$\frac{dA_z(t)}{dt} \leq -u_z^a A_z(t) + \frac{C_2 \delta}{h_2}$$

and therefore

$$\bar{A}_z \leq \frac{C_2 \delta}{h_2 u_z^a}.$$

Also for t large enough, by $A_z(t) < \delta$ and (39) we find that

$$\frac{dA_x(t)}{dt} \geq -u_x^a A_x(t) + \exp[-(u_x^l + e_2 \sigma_2 \delta) \tau_x] B(A_x(t - \tau_x)).$$

By assumption (24), if δ is small enough, then there exists $A_x^{**}(\delta) > 0$ such that

$$\exp[-(u_x^l + e_2 \sigma_2 \delta) \tau_x] B(A) > u_x^a A \quad \text{when } 0 < A < A_x^{**}(\delta);$$

$$\exp[-(u_x^l + e_1 \sigma_1 \delta) \tau_x] B(A) < u_x^a A \quad \text{when } A > A_x^{**}(\delta).$$

Moreover, $A_x^{**}(\delta) \rightarrow A_x^{**}$ when $\delta \rightarrow 0$. Since $B(\cdot)$ is increasing, we may apply a comparison argument similar to that described in the proof of Theorem 4.1 to conclude that

$$\underline{A}_x := \liminf_{t \rightarrow \infty} A_x(t) \geq A_x^{**}(\delta). \quad (71)$$

For t large enough, we have $A_z(t) < \delta$. By (71) and the monotonicity of function $B(\cdot)$, taking the limit inferior as $t \rightarrow \infty$ in system(39), we obtain

$$\underline{L}_x \geq \frac{B(A_x^{**}(\delta))}{u_x^l + e_2 \sigma_2 \delta} \exp[1 - (u_x^l + e_2 \sigma_2 \delta) \tau_x] := L_x^{**}(\delta). \quad (72)$$

where $\underline{L}_x = \liminf_{t \rightarrow \infty} L_x(t)$. Note that $L_x^{**}(\delta) \rightarrow L_x^{**}$ as $\delta \rightarrow 0$. From (72), $L_x(t) \geq L_x^{**}(\delta) - \delta$ for t large enough. By (21), we obtain the following inequality

$$L_y(t) \geq A_z(0) \exp \left[\int_0^t \left(-u_z^a + \frac{C_2 e_2 \sigma_2 (L_x^{**}(\delta) - \delta)}{1 + h_2 e_2 \sigma_2 (L_x^{**}(\delta) - \delta)} \right) ds \right]. \quad (73)$$

For δ involved above, then inequality

$$\frac{C_2 e_2 \sigma_2 (L_x^{**}(\delta) - \delta)}{1 + h_2 e_2 \sigma_2 (L_x^{**}(\delta) - \delta)} > u_z^a$$

holds for the condition (68). Therefore, $A_z(t)$ grows exponentially, which leads to a contradiction with (70).

The above claim shows that both $F_1(0, 0, 0)$ and $F_2(L_x^{**}, A_y^{**}, 0)$ are uniform weak repellers for F_0 in the sense that

$$\limsup_{t \rightarrow \infty} \|\psi(t)\varphi - F_i\| \geq \delta \quad \text{for all } \varphi \in F_0, i = 1, 2,$$

with the maximum norm $\|\cdot\|$. Define a continuous function $r : F \rightarrow R_+$ by

$$r(\varphi) = \min(\varphi_1(0), \varphi_2(0), \varphi_3(0)) \quad \text{for all } \varphi = (\varphi_1, \varphi_2, \varphi_3) \in F.$$

Thus, r is a generalized distance function for the semiflow $\psi(t)$ (see Definition 1.3.1 of Zhao, 2003). It then follows from Theorem 1.3.2 of Zhao (2003) that there exists a constant $\xi > 0$ such that $\min\{r(\beta) : \beta \in \omega(\varphi)\} > \xi$ for any $\varphi(\theta) \neq 0$ on $[-\tau_x, 0]$. Hence,

$$\liminf_{t \rightarrow \infty} L_x(t) \geq \xi, \quad \liminf_{t \rightarrow \infty} A_x(t) \geq \xi, \quad \liminf_{t \rightarrow \infty} A_z(t) \geq \xi$$

uniformly for all solutions of the system (39) with $A_x(\theta) \neq 0$ on $[-\tau_x, 0]$. This completes the proof of Theorem 4.3.

4.4 The persistence of the whole system

In the following, we show that the system (22) is permanent. Because of the mechanism that the parasitism between crow chicks and cuckoo nestlings can benefit crows chicks by deterring the visitation of the predator cats to the nests of the crows.

First, by the Theorem 3.1, we know that the solution of system (22) or (23) is upper bounded in the sense that there exists a constant $\zeta > 0$ such that

$$\limsup_{t \rightarrow \infty} x_i(t) < \zeta, \quad i = 1, 2, 3, 4, 5$$

for all solutions $x(t) = (L_x, A_x, L_y, A_y, A_z)$ of system (22) or (23) and with $A_x(\theta) \neq 0, \theta \in [-\tau_x, 0]$. Then, we will verify that under conditions (74) and (75) the system(22) is uniformly and weakly persistent.

Theorem 4.4. *Suppose that (24), (74) and (75) hold, then the system (22) or (23) is uniformly and weakly persistent for all nonnegative solutions with $A_x(\theta) \neq 0$ on $[-\tau_x, 0]$.*

Where

$$\frac{C_1 e_1 \sigma_1 L_x^{**}}{\tau_y (1 + h_1 e_1 \sigma_1 L_x^{**})} [1 - \exp(-u_y^l \tau_y)]^2 > (u_y^l)^2 \quad (74)$$

and

$$\frac{C_2 e_2 \sigma_2 L_x^{**}}{1 + h_2 e_2 \sigma_2 L_x^{**}} > u_z^a. \quad (75)$$

Proof. First of all, we prove that there exists a constant $\epsilon_1 > 0$ such that for all solutions $(L_x, A_x, L_y, A_y, A_z)$ of the system (22) with $A_x(\theta) \neq 0$ on $[-\tau_x, 0]$, we have

$$\limsup_{t \rightarrow \infty} L_y(t) \geq \epsilon_1, \quad \limsup_{t \rightarrow \infty} A_z(t) \geq \epsilon_1.$$

Suppose the claim is not true, then for any $\epsilon_1 > 0$ there exists solution $L_y(t), A_y(t)$ with

$$\bar{L}_y < \epsilon_1, \quad \bar{A}_z < \epsilon_1 \quad (76)$$

where $\bar{L}_y = \limsup_{t \rightarrow \infty} L_y(t), \bar{A}_z = \limsup_{t \rightarrow \infty} A_z(t)$. Because the inequality (73) holds, $L_y < \epsilon_1$ and $A_z < \epsilon_1$ for all t sufficiently large. Since the integrand of the integral term in (20) increases with $L_x(\xi)$,

we obtain

$$\begin{aligned}\frac{dA_y(t)}{dt} &\leq -u_y^a A_y(t) + \frac{C_1 \epsilon_1}{h_1 \tau_y} \int_{t-2\tau_y}^{t-\tau_y} \exp[-u_y^l(t-\xi)] d\xi \\ &\leq -u_y^a A_y(t) + \frac{C_1 \epsilon_1}{h_1}\end{aligned}$$

and therefore

$$\bar{L}_y \leq \frac{C_1 \epsilon_1}{h_1 u_y^a}.$$

Also for t sufficiently large, by $L_y(t) < \epsilon_1$, $A_z(t) < \epsilon_1$ and (12), we obtain

$$\frac{dA_x(t)}{dt} \geq -u_x^a A_x(t) + \exp[-(u_x^l + e_1 \sigma_1 \epsilon_1 + e_2 \sigma_2 \epsilon_1) \tau_x] B(A_x(t - \tau_x)).$$

By assumption (24), if ϵ_1 is sufficiently small, then there exists $A_x^{**}(\epsilon_1) > 0$ such that

$$\exp[-(u_x^l + e_1 \sigma_1 \epsilon_1 + e_2 \sigma_2 \epsilon_1) \tau_x] B(A) > u_x^a A \quad \text{when } 0 < A < A_x^{**}(\epsilon_1);$$

$$\exp[-(u_x^l + e_1 \sigma_1 \epsilon_1 + e_2 \sigma_2 \epsilon_1) \tau_x] B(A) < u_x^a A \quad \text{when } A > A_x^{**}(\epsilon_1).$$

Moreover, $A_x^{**}(\epsilon_1) \rightarrow A_x^{**}$ when $\epsilon_1 \rightarrow 0$. Since $B(\cdot)$ is increasing, applying a comparison argument similar to that described in the proof of Theorem 4.1 leads us to conclude that

$$\underline{A}_x := \liminf_{t \rightarrow \infty} A_x(t) \geq A_x^{**}(\epsilon_1). \quad (77)$$

For t large enough, we have $L_y(t) < \epsilon_1$ and $A_z(t) < \epsilon_1$. By (77) and the monotonicity of the function $B(\cdot)$, taking the limit inferior as $t \rightarrow \infty$ in the (11), we obtain

$$\underline{L}_x \geq \frac{B(A_x^{**}(\epsilon_1))}{u_x^l + e_1 \sigma_1 \epsilon_1 + e_2 \sigma_2 \epsilon_1} \exp[-(u_x^l + e_1 \sigma_1 \epsilon_1 + e_2 \sigma_2 \epsilon_1) \tau_x] := L_x^{**}(\epsilon_1). \quad (78)$$

where $\underline{L}_x = \liminf_{t \rightarrow \infty} L_x(t)$. Note that $L_x^{**}(\epsilon_1) \rightarrow L_x^{**}$ as $\epsilon_1 \rightarrow 0$. From (78), $L_x(t) \geq L_x^{**}(\epsilon_1) - \epsilon_1$ for t sufficiently large. Since the integrand in the (19) increases with $L_x(\xi)$, we obtain

$$L_y(t) \geq \frac{C_1}{\tau_y} \int_{t-\tau_y}^t \int_{\theta-\tau_y}^{\theta} \exp[-u_y^l(t-\xi)] \frac{e_1 \sigma_1 (L_x^{**}(\epsilon_1) - \epsilon_1) L_y(\xi)}{1 + h_1 e_1 \sigma_1 (L_x^{**}(\epsilon_1) - \epsilon_1)} d\xi d\eta. \quad (79)$$

We now show that $L_y(t)$ grows exponentially with t , which contradicts with (76). From the characteristic equation of the integral equation (79) (changing \geq to $=$)

$$(u_y^l + \lambda)^2 = \frac{C_1 e_1 \sigma_1 (L_x^{**}(\epsilon_1) - \epsilon_1)}{\tau_y (1 + h_1 e_1 \sigma_1 (L_x^{**}(\epsilon_1) - \epsilon_1))} \{1 - \exp[-(\lambda + u_y^l) \tau_y]\}^2, \quad (80)$$

we can choose a constant ϵ_1 small enough such that

$$(u_y^l)^2 < \frac{C_1 e_1 \sigma_1 (L_x^{**}(\epsilon_1) - \epsilon_1)}{\tau_y (1 + h_1 e_1 \sigma_1 (L_x^{**}(\epsilon_1) - \epsilon_1))} [1 - \exp(-u_y^l \tau_y)]^2, \quad (81)$$

which is possible because of the condition (74). By (81), the left-hand side of (80) is less than the right-hand side when $\lambda = 0$. Since the left-hand side grows without bound with λ while the right-hand side tends to a constant, it follows that (80) has a positive real root. Therefore, $L_y(t)$ grows exponentially, which leads to a contradiction with (76).

At the same time, from equation (21), we obtain

$$\frac{dA_z(t)}{dt} \leq -u_z^a A_z(t) + \frac{C_2 e_2 \sigma_2 (L_x^{**}(\epsilon_1) - \epsilon_1) A_z(t)}{1 + h_2 e_2 \sigma_2 (L_x^{**}(\epsilon_1) - \epsilon_1) + k_2 \epsilon_1}$$

and therefore

$$A_z(t) \geq A_z(0) \exp \left[\int_0^t \left(-u_z^a + \frac{C_2 e_2 \sigma_2 (L_x^{**}(\epsilon_1) - \epsilon_1)}{1 + h_2 e_2 \sigma_2 (L_x^{**}(\epsilon_1) - \epsilon_1) + k_2 \epsilon_1} \right) ds \right].$$

For ϵ_1 involved above, we have that

$$\frac{C_2 e_2 \sigma_2 (L_x^{**}(\epsilon_1) - \epsilon_1)}{1 + h_2 e_2 \sigma_2 (L_x^{**}(\epsilon_1) - \epsilon_1) + k_2 \epsilon_1} > u_z^a$$

holds for the condition (75). Therefore, $A_z(t)$ grows exponentially, which contradicts with (76). This completes the proof of Theorem 4.4.

5 Numerical simulation

In this section, numerical simulations are conducted to demonstrate our analytical results. Suppose the hatching rate for crows is chosen as $B(A_x) = \frac{bA_x}{1+cA_x}$, where the parameter c depends on the nest type. Female crows mate and lay eggs throughout their lives. Individual females appear to be capable of laying between 65 and 91 eggs in one year (Canestrari et al., 2014). Moreover, given the assumption that 50% of crow adults are females, we chose to use a monthly fecundity rate of $b=6$. Other parameter values are taken from Table 1 and additional values are listed in the caption of each figure. In all the simulations, we consider the time in months.

Table 1: Values of the parameters

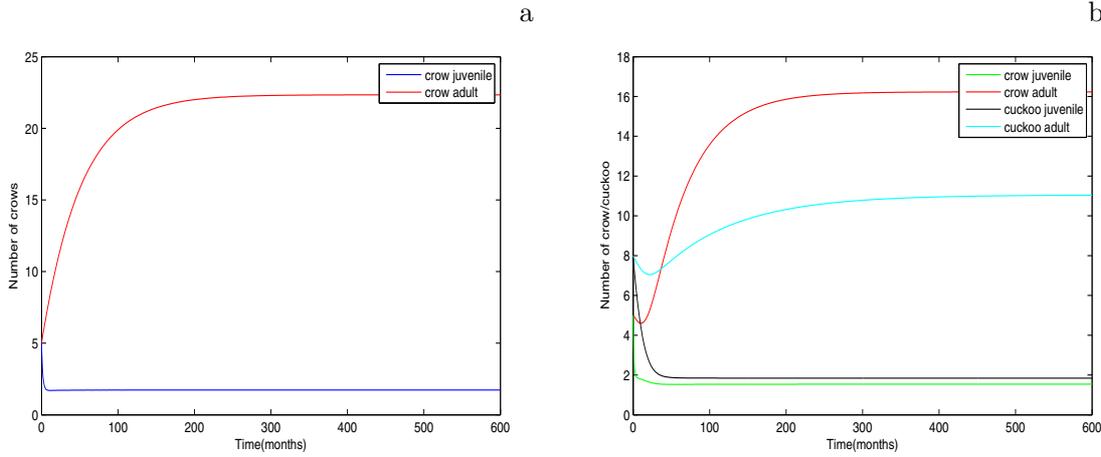


Figure 1: (a): The time series of the solution of system (28), here the initial values: $L_x(0) = 5, A_x(0) = 5, c = 4$. Other parameters are obtained from Table 1. (b): The time series of the solution that is cat free, here the initial values are: $L_x(0) = 5, A_x(0) = 5, L_y(0) = 8, A_y(0) = 8, c = 4$. Other parameters are obtained from Table 1

Symbol	value	Reference
u_x^l	0.6	Bolopo et al. (2015)
u_x^a	0.02	Bolopo et al. (2015)
u_y^l	0.34	Canestrari et al. (2014)
u_y^a	0.01	Bolopo et al. (2015)
u_z^a	0.04	Bolopo et al. (2015)
e_1	0.43	Canestrari et al. (2014)
e_2	0.04	Canestrari et al. (2014)
σ_1	1	Canestrari et al. (2014)
σ_2	0.4	Canestrari et al. (2014)
h_1	0.28 months	Bolopo et al. (2015)
h_2	0.18 months	Bolopo et al. (2015)
k_2	0.5	Wang (2016)
τ_x	2 months	Bolopo et al. (2015)
τ_y	2.5 months	Canestrari et al. (2014)
b	6	Canestrari et al. (2014)
c	-	-
C_1	0.60	-
C_2	0.32	-

For the numerical simulations in Fig.1 (a), we choose parameter values satisfying Theorem 4.1. Both Fig.1 (a) and Theorem 4.1 show that a cuckoo-cat free equilibrium is globally asymptotically stable when $D_0 < 1$ and $D_1 < 1$, where $D_0 = \frac{(C_1 e_1 \sigma_1)(1 - \exp\{-u_y^l \tau_y\})^2}{\tau_y(1 + h_1 e_1 \sigma_1 L_x^{**})(u_y^l)^2}$ and $D_1 = \frac{C_2 e_2 \sigma_2 L_x^{**}}{(1 + h_2 e_2 \sigma_2 L_x^{**})u_z^a}$. Moreover, the coexistence of crows and cuckoos is illustrated in Fig.1 (b) when we choose parameter values satisfying Theorem 4.2 with $D_0 > 1$.

Furthermore, we choose parameter values from Table 1 satisfying Theorem 4.3, and additional values

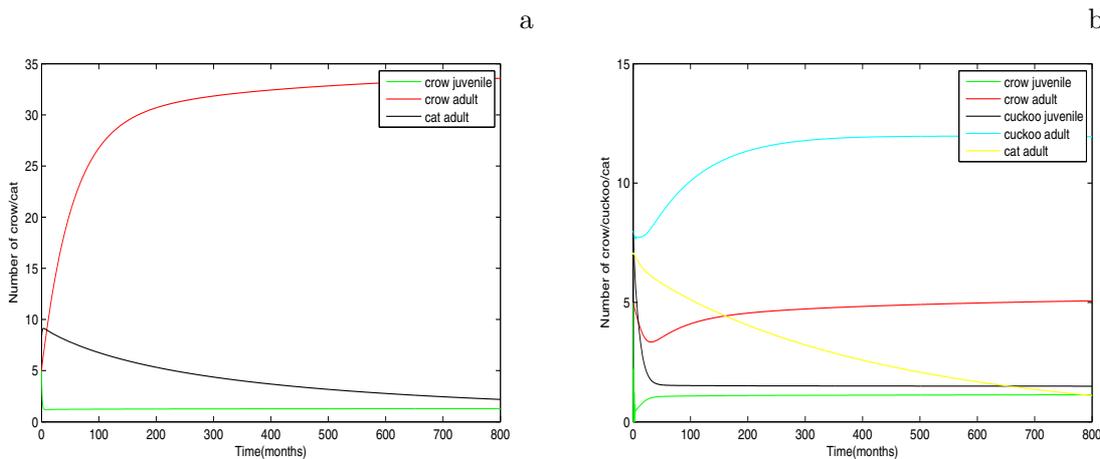


Figure 2: (a): The time series of the solution of system (30), here the initial values: $L_x(0) = 5, A_x(0) = 5, A_z(0) = 8, c = 4, \tau_x = 2$. Other parameters are obtained from Table 1. (b): The time series of the solution with the whole system, here the initial values: $L_x(0) = 5, A_x(0) = 5, L_y(0) = 8, A_y(0) = 8, A_z(0) = 7, c = 4, \tau_y = 2.5, k_2 = 0.5$. Other parameters are obtained from Table 1.

are listed in the caption of the figure. From the numerical simulations in Fig.2 (a), we can easily see that both Fig.2 (a) and Theorem 4.3 show that the cuckoo-free equilibrium is globally asymptotically stable when $D_1 > 1$. Similarly, we choose parameter values satisfying Theorem 4.4 with $D_0 > 1$ and $D_1 > 1$. Then, from Fig.2 (b), we can see the coexistence of crows, cuckoos and cats.

To study the influence of the maturation time delay τ_x on the dynamics among cuckoos, crows and cats, we get Fig.3. From Fig.3, we can see that if $\tau_x \in (1.5, 3.5)$, approximately, the vertical amplitudes of $L_x(t), A_z(t)$ and $L_y(t)$ are as small as a point, suggesting that they are asymptotically stable; if τ_x increases by an interval $(3.5, 4]$, approximately, the vertical amplitudes of $L_x(t), L_y(t)$, and $A_z(t)$ will become increasing larger, showing that they become more and more unstable. As we know that τ_x represents the maturation time of the crow chicks, the change of the τ_x will change the dynamics among cuckoos, crows and cats. Similarly, the impact of the maturation time delay τ_y on the dynamics among cuckoos, crows, and cats is studied by numerical simulations in Fig.4. As shown in Fig.4, an increase of τ_y from 1.5 to 4 has similar "destabilizing" effects on the dynamics of the system to those of τ_x : when $\tau_x = 2.5$, for $\tau_y \leq 3$, approximately, the vertical amplitudes of $L_x(t)$ and $L_y(t)$ are as small as a point, suggesting that they are asymptotically stable; when $\tau_y \geq 3$ approximately, the vertical amplitudes of $L_x(t)$ and $L_y(t)$ will be larger, showing that they become increasing unstable. Moreover, the vertical amplitudes of $A_y(t)$ are as small as a point with $\tau_y \in [1.5, 4]$, and when $\tau_y = 2.5$, approximately, the vertical amplitudes of $A_y(t)$ reaches its the greatest value and then decreases with $\tau_y \in [2.5, 4]$, approximately. As we know that τ_x represents the maturation time of the crow chicks, the change of the τ_x will change the dynamics among cuckoos, crows and cats. Biologically, this means that a shorter immature to maturation period is helpful for the adults.

Lastly, Fig.5 shows the stability change of the crow chicks and the cuckoo nestlings as τ_x and τ_y simultaneously increase from 0 to 12 (Here, 12 represents 120 days, i.e., 4 months). It seems clear that crow chicks are stable as $(\tau_x, \tau_y) \in (0, 9) \times (0, 12]$ approximately. For $(\tau_x, \tau_y) \in (9, 12] \times (0, 12]$ is unstable.

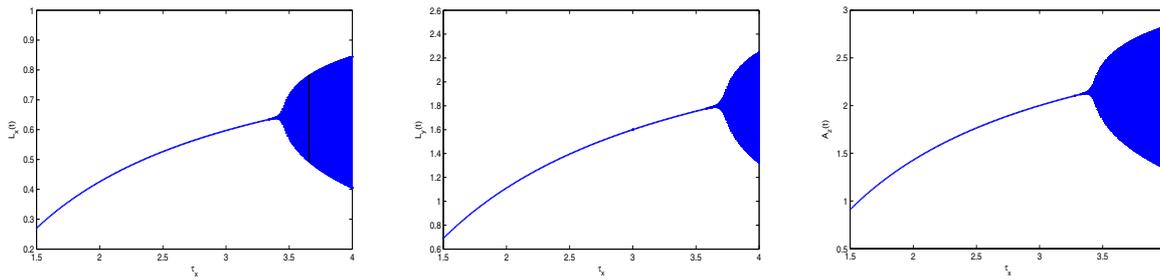


Figure 3: The ultimate oscillation interval of the solution to the system (22), when τ_x increases from 1.5 to 4, here $\tau_y = 2.5$ (month), $t \in [0, 800]$, $c = 4$, other parameters are obtained from Table 1. These figures show that the influence of the maturation time delay τ_x on the dynamics among cuckoos, crows and cats.

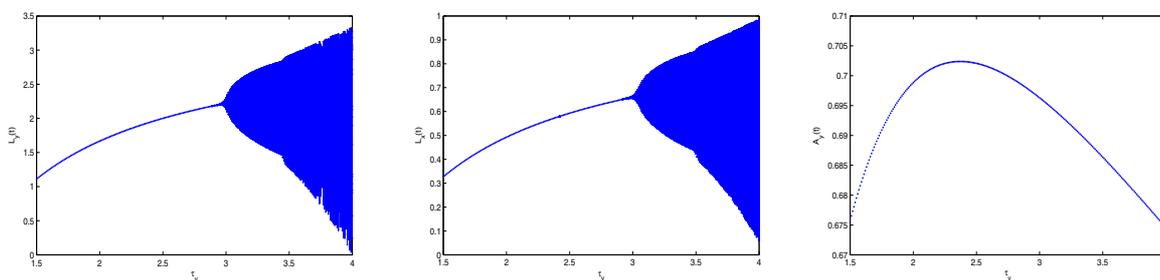


Figure 4: The ultimate oscillation interval of the solution to the system (22), when τ_y increases from 1.5 to 4, here $\tau_x = 2$ (month), $t \in [0, 800]$, $c = 4$, other parameters are obtained from Table 1. These figures show that the influence of the maturation time delay τ_y on the dynamics of cuckoos and crows.

For the cuckoo nestlings, vertical amplitudes of the cuckoo nestlings smaller as τ_x decreases from 9 to 0, suggesting that when τ_x is small, the cuckoo nestlings are stable. These results is consistent with the results of Figure 3 and Figure 4.

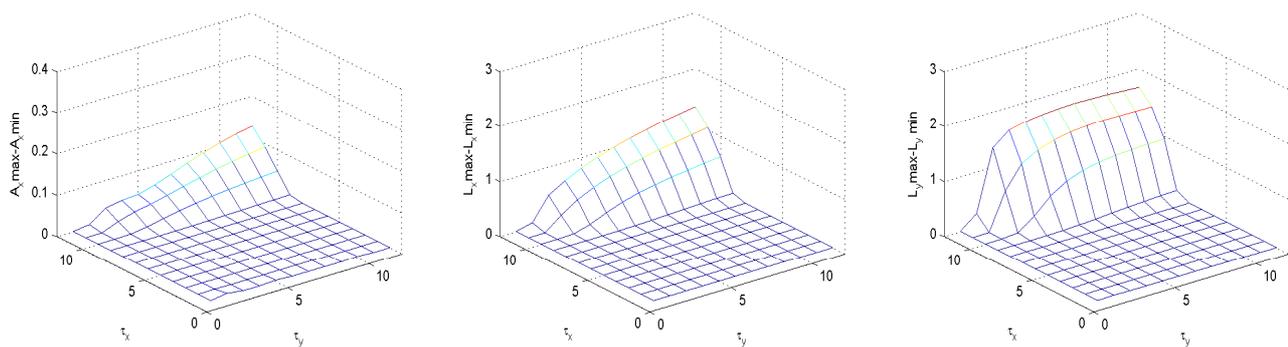


Figure 5: The ultimate oscillation interval of the solution to the system (22) according to increase of τ_x, τ_y , here $t \in [0, 800]$, $c = 4$, other parameters are obtained from Table 1. These figures show that the influence of the maturation time delay τ_x and τ_y on the dynamics among cuckoos, crows and cats.

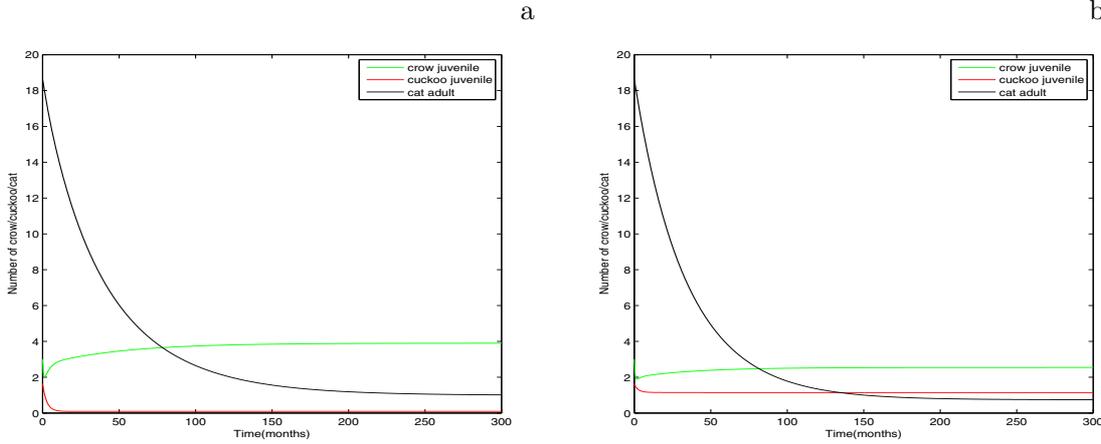


Figure 6: (a): The time series of the solution of system (82), here the initial values: $L_x(0) = 2.9988$, $L_y(0) = 1.6352$, $A_z(0) = 18.6139$, $\tau_y = 0$. Other parameters are obtained from Table 2. (b): The time series of the solution of system (82), here the initial values: $L_x(0) = 2.9988$, $L_y(0) = 1.6352$, $A_z(0) = 18.6139$, $\tau_y = 2.5$. Other parameters are obtained from Table 2.

6 Summary and discussion

In this paper, motivated by the works Canestrari et al.(2014), Wang (2016) and Lou et al. (2017), we take stage structure into account and propose a stage-structured mutualism-parasitism-predation model to investigate the impacts of maturation time delays on the dynamics among cuckoos, crows and cats. Firstly, we obtain the conditions to guarantee the existence of equilibrium for the individual subsystems. Then, the conditions to guarantee the globally asymptotical stabilities of the cuckoo-cat-free equilibrium and the uniform persistence of the whole system are obtained. More specifically, we show that the cuckoo-cat-free equilibrium (i.e., only crows) is globally asymptotically stable if $D_0 < 1$, $D_1 < 1$ (Theorem 4.1 and Fig.1 (a)), and the whole system uniformly persist if $D_0 > 1$, $D_1 > 1$ (Theorem 4.4 and Fig. 2 (b)).

In order to compare this with system (1) in Wang (2016) and study the effect of the maturation time delays on the dynamics among crow chicks, cuckoo nestlings and cat adults, we rewrite our model such that it is free of adult crows and cuckoos:

$$\begin{cases} \frac{dL_x(t)}{dt} = -u_x^l L_x(t) - \frac{e_1 \sigma_1 L_x(t) L_y(t)}{1 + h_1 e_1 \sigma_1 L_x(t)} - \frac{e_2 \sigma_2 L_x(t) A_z(t)}{1 + h_2 e_2 \sigma_2 L_x(t) + k_2 L_y(t)} \\ \frac{dL_y(t)}{dt} = -u_y^l L_y(t) + \frac{C_1}{\tau_y} \int_{t-\tau_y}^t \exp[-u_y^l(t-\xi)] \frac{e_1 \sigma_1 L_x(\xi) L_y(\xi)}{1 + h_1 e_1 \sigma_1 L_x(\xi)} d\xi \\ \frac{dA_z(t)}{dt} = -u_z^a A_z(t) + \frac{C_2 e_2 \sigma_2 L_x(t) A_z(t)}{1 + h_2 e_2 \sigma_2 L_x(t) + k_2 L_y(t)}. \end{cases} \quad (82)$$

In (82), we find the intrinsic growth rate of $L_x(t)$ is zero in the absence of crow adults. But in order to compare this system (1), we take some parameters as in Table 2 and keep the same biological meaning of parameters as in (1) in Wang (2016).

Table 2: Values of the parameters

Parameters	Value	Reference	Parameters	Value	Reference
u_x^l	0.6	Wang (2016)	u_x^a	0.02	Wang (2016)
u_y^l	0.34	Wang (2016)	u_y^a	0.01	Wang (2016)
u_z^a	0.04	Wang (2016)	e_1	0.43	Wang (2016)
e_2	0.04	Wang (2016)	σ_1	1	Wang (2016)
σ_2	0.4	Wang (2016)	h_1	0.28 months	Wang (2016)
h_2	0.18 months	Wang (2016)	k_2	0.5	Wang (2016)
τ_x	2 months	Wang (2016)	τ_y	2.5 months	Wang (2016)
c	-	-	b	6	Wang (2016)
C_1	0.60	-			

Based on the above consideration, we get Fig.6(a) with $\tau_y = 0$ and take the same parameters values as in (1). By contrasting Fig.6(a) with Fig.6 in Wang (2016), we find the population numbers are almost the same. Then we take $\tau_y = 2.5$ with the other parameters value unchanged, and we get Fig.6(b). We find the number of the cuckoo nestlings increase as the maturation time delay increases, and the number of cat adults decreases due to the deterrence by cuckoo nestlings. The number of crow chicks decreases as the number of cuckoo nestlings increases.

Theorem 4.4 indicates that when an appropriate control agent is helpful to making the net reproduction number of predators D_0 and D_1 larger than 1, the whole system will uniformly persist. Possible control agents include the high conversion efficiencies C_1 and C_2 (but are not limited to those), a low handling time h_1 and h_2 (but are not limited) and a moderate maturation time τ_y . Note that $D_0 > 1$ is not satisfied if τ_y is large or τ_y is small since the left-hand side of $D_0 > 1$ is $O(\tau_y)$ as $\tau_y \rightarrow 0$. Thus, the cuckoos can survive only if their nestling development time is neither too long nor too short. If the development time is too long, not enough cuckoos will mature. If it is too short, the ecological interpretation indicates that not enough cuckoo nestlings will exist to protect the crow chicks and the nestlings fail to consume enough crow biomass.

The main purpose of this paper is to find the impacts of the maturation time delays τ_x and τ_y on the dynamics among crows, cuckoos and cats. It is shown that the maturation period of the immature crows τ_x and immature cuckoos τ_y largely determine the stabilities of the crow chicks and cuckoo nestlings (Fig.4, Fig.5). Moreover, as shown in Fig.4, as τ_x increases from 3 to 4, the crow chick and cuckoo nestling populations may lose their stabilities and become increasingly unstable due to the enlarged amplitudes of the oscillation intervals. Biologically, this means that a shorter maturation period of crow chicks is helpful to stabilizing the system. Of course, this results that the maturation time and age-structure may change the stability of the system is not only the first time to be obtained. There are many works about stage-structure systems have shown that the maturation time may change the stability of the system. For example, in Hastings, 1984 a discrete predator-prey model in which the predator consumes only juvenile prey was developed. It was shown that an age-dependent predation can have a stabilizing effect and that the behavior of the model depends critically on the duration of maturation period of the prey, in

particular, a very small number of elderly prey represent a powerful stabilizing factor. Additionally, May, (1974) and Smith, (1974) developed models for the predator-prey interactions with discrete age structure of prey, which lead to changes in stability. Therefore, the introducing of the maturation can indeed improve our understanding of the system.

In a word, a parasitism-mutualism-predation model with stage structure is more complicated than systems with no stage structure. The former includes various properties and phenomena that can hardly be embodied by the latter but are very consistent with real ecosystems, which helps us interpret the diversity and many phenomena of ecosystems.

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