



## Original Research Article

# Stage-structured ratio-dependent predator–prey models revisited: When should the maturation lag result in systems' destabilization?

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## ABSTRACT

Time delay is often introduced into models of theoretical ecology to take into account stage structuring of real populations. The well-known characteristic benchmark of time delay models is eventual destabilization of systems' equilibria for a sufficiently large maturation/gestation time period. Here we argue, however, that some delay formulations might lack a sound biological rationale and, more importantly, the use of different delay formulations in models might result in rather different outcomes in terms of stability loss. To illustrate this idea we consider a family of predator–prey models with a ratio-dependent predator functional response with a maturation time lag of predators. In such models the functional response depends on the ratio between the predators and the available prey as opposed to a prey-dependent functional response. To describe the effects of delay, we use two different formulations from the literature: one based on the work by Beretta and Kuang (1996), which we call the conventional approach, with delay being included only into the per-capita numerical response of predator. The other formulation is the Wangersky–Cunningham (1957) approach, where delay is introduced in the overall predator numerical response. Unlike the previous studies, we focus here on deriving the explicit conditions of stability of the interior equilibrium (assuring species coexistence) in the presence of delay in terms of model parameters. We investigate three scenarios of prey growth rate parametrization: (i) the prey growth is given by the logistic function, (ii) the prey growth is subject to a strong Allee effect and (iii) there is a weak Allee effect in prey. In the latter two cases the per capita growth rate is an increasing function at low prey density. We show that the use of the two above delay formulations eventually result in completely different outcomes: with the conventional approach, the interior predator–prey equilibrium will be eventually destabilized for a supercritical time lag, whereas, implementation of the Wangersky–Cunningham approach predicts an absolute stability of the equilibrium within a large range of parameters, i.e. the system cannot be destabilized by means of delay. We find that for the models parameters, where delay-induced destabilization in the system with an Allee effect is possible (the interior equilibrium is conditionally stable), the stability loss eventually results in population collapse and extinction of both species.

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## 1. Introduction

Real populations usually pass through a number of stages during their life cycle with completely different morphology. To acknowledge this fact, time delay has been introduced into models of theoretical ecology. In particular, it is often important to take into account the processes of gestation and maturation to make an abstract model more biologically realistic (Kuang, 1993; May, 2001; Murdoch et al., 2003). The characteristic property of population models with a time delay is their oscillatory behavior:

for a sufficiently large maturation period, an initially stable equilibrium becomes unstable and the system exhibits sustained oscillations (Kuang, 1993; Ruan, 2009). Interestingly, delay-induced destabilization and oscillations can be observed even in single species models (Murray, 1989; Kuang, 1993; May, 2001). In predator–prey/consumer–resource models based on ODEs, a discrete time delay can be introduced in various ways. For instance, in a standard predator–prey model the maturation of predators (as well as the effects of gestation) is often parameterized as follows (Kuang, 1993; Beretta and Kuang, 1996; Ruan, 2009):

$$\frac{dx(t)}{dt} = x(t)r(x(t)) - f(x(t), y(t))y(t), \quad (1)$$

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$$\frac{dy(t)}{dt} = y(t)(\phi f(x(t-\tau), y(t-\tau)) - \delta(y(t))), \quad (2)$$

where  $x$  and  $y$  are the densities of prey and predator, respectively at time  $t$ ;  $\tau$  is the time delay parameter, describing effects of gestation/maturation. The function  $f$  is the predator functional response;  $r$  is the per capita growth rate of prey;  $\delta$  is the mortality rate of predator; the parameter  $\phi$  ( $0 < \phi < 1$ ) stands for the conversion efficiency of food consumption.

Model (1)–(2) with various parameterizations of functions  $r(x)$ ,  $f(x, y)$  and  $\delta(y)$  has been studied quite extensively in the literature (e.g. some modifications of Eqs. (1)–(2) considered a time lag in  $r(x)$  and/or  $\delta(y)$ ); a complete list of all references might include hundreds of publications (for insightful reviews see Kuang, 1993; Ruan, 2009). The most important general result seems to be that initially stable system (1)–(2) with  $\tau=0$  would be eventually destabilized for a supercritical maturation period  $\tau$ . In this paper, we shall call the approach of representing maturation of predators based on Eq. (2) the conventional approach, since it has been dominant in the literature until very recently.

Surprisingly enough, much less attention has been paid to the ecological interpretation of the way of including the time delay in the predator numerical response of form  $y(t)f(x(t-\tau), y(t-\tau))$ . Indeed, consider as a paradigm the scenario where there are only two life stages within a predator population: juveniles and adults – in particular, by ‘juveniles’ one can understand eggs or larvae. Adults become mature after period  $\tau$  (the same reasoning is applicable when modelling effects of gestation). Assume that in the model  $y$  describes only adults and that juveniles have another source of food. It logically follows that the replenishment of adults at time  $t$  should depend only on the number of juveniles which were born at time  $t-\tau$ , and not on the current population of adults at time  $t$  as it is the case in Eq. (2). Thus the numerical response term  $y(t)f(x(t-\tau), y(t-\tau))$  seems to lack some biological rationale.

Gourley and Kuang (2004) suggest the following parameterization to model the effects of maturation/gestation

$$y(t-\tau) f(x(t-\tau), y(t-\tau)) \exp(-\delta_j \tau). \quad (3)$$

In this case, new adults come from the juveniles produced at time  $t-\tau$ , and to take into account eventual mortality of juveniles, we need to multiply the numerical response by the multiplier  $\exp(-\delta_j \tau)$ , where  $\delta_j$  is the mortality of juveniles (Wang and Chen, 1997). This parameterization seems to be more sound since it has a clear biological interpretation. Note that the same logic is applicable to SIR type models in epidemiology when one wishes to include latent periods in the transmission of infectious disease (Beretta and Kuang, 2001; Xiao and Chen, 2001). In this case the ‘predators’ in the delay model will correspond to infected individuals, spreading disease, and the ‘prey’ will correspond to healthy susceptible organisms.

Interestingly, an idea similar to representation (3) was initially suggested much earlier by Wangersky and Cunningham (1957), who proposed the following way of incorporating the maturation delay of predators into models:

$$\frac{dy(t)}{dt} = \phi f(x(t-\tau), y(t-\tau)) y(t-\tau) - \delta y(t). \quad (4)$$

Formulation (4) can be considered as a particular case of Eq. (3), where the mortality of juveniles (or eggs) is very small compared to the maturation period such that  $\delta_j \tau \ll 1$ . Biologically this can signify that eggs are laid in safe places/refuges with an efficient protection from predators. Alternatively, for a fixed  $\tau$  we can include the exponential mortality term in Eq. (3) into the coefficient  $\phi$ . The model consisting of Eqs. (1) and (4) is known in the literature as the Wangersky–Cunningham delay formulation (Ruan, 2001).

In earlier theoretical works, the conventional delay formulation was predominant (note that this approach stems from the classical work by Volterra (1926) on the distributed delay models based on integro-differential equations), but in recent years the delay formulation by Wangersky and Cunningham and its extension by Gourley and Kuang (2004) are getting more popularity because of their straightforward biological interpretations. The conventional approach Eq. (2) is still widely used in the recent literature, however (e.g. Fan and Li, 2007; Gakkhar et al., 2009; Meng et al., 2011; Xu et al., 2012 and many other publications).

The use of a delay modelling approach without a clear biological background may potentially result in erroneous predictions and wrong conclusions. As an illustrative example, we investigate here a family of ratio-dependent predator–prey models with predators’ maturation lag using two delay representation approaches: the conventional and the Wangersky–Cunningham formulations. In the ratio-dependent functional response the food intake by the predator is a function of the ratio between the prey to predator abundance/biomass. This type of functional response has been supported by a number of empirical data (Arditi et al., 1991; Reeve, 1997; Bishop et al., 2006) and is supposed to be more ecologically relevant compared to the ‘classical’ prey dependent functional response: its implementation does not result in the paradox of enrichment, for instance (Arditi and Ginzburg, 1989; Arditi et al., 1991; Berezovskaya et al., 2001).

Overall, ratio-dependent models with delay have been extensively considered in the literature for both delay modelling approaches; however, those studies were limited to the case of the logistic growth of prey only (Beretta and Kuang, 1998; Fan and Wang, 2001; Xiao and Li, 2002; Kovacs et al., 2009; Wang and Pei, 2011; Sarwardi et al., 2012). In particular, the ecologically important case, where the prey growth is affected by an Allee effect has not been addressed. The Allee effect in population growth is a rather widespread phenomenon, in which the per capita growth rate function  $r(x)$  increases at small species density  $x$  (Allee, 1931; Courchamp et al., 1999; Berec et al., 2007) and it may arise due to various ecological mechanisms (Stephens and Sutherland, 1999; Berec et al., 2007; Courchamp et al., 2008). Thus, understanding of effects of delay in systems with the Allee effect would be an important extension of the previous studies with the standard assumption of the logistic growth of prey.

The main focus in the earlier works on delay models was on revealing the conditions of delay-induced destabilization of equilibrium for a certain critical  $\tau$  (often in term of obtaining sufficient conditions for destabilization). In our paper, we are interested in deriving the explicit stability conditions in terms of the model parameters for both delay formulations and for various cases of parametrization of the prey growth: (i) logistic growth; (ii) strong Allee effect; (iii) weak Allee effect. In each case we analytically derive the stability conditions for the interior equilibrium in the presence of delay. We compare the effects of maturation delay on the stability of the interior equilibrium for the two delay approaches with different growth rate functions of prey, and we show that the use of the different delay formulations results in qualitatively different predictions. In particular, for the conventional delay approach there will always exist a supercritical time delay which eventually destabilizes a locally stable coexistence equilibrium, whereas for the Wangersky–Cunningham approach, the equilibrium might remain absolutely stable, i.e. it will be stable for any value of  $\tau$ , other parameters being fixed. We find that the absolute stability in ratio-dependent models with the Allee effect in the prey can be considered as a sort of lifeboat mechanism. Indeed, unlike in the systems with logistic growth, the delay-induced destabilization in the presence of the Allee effect takes place via a subcritical Hopf bifurcation with an further density collapse and eventual extinction of both species.

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