



Application of a delayed logistic equation to a reindeer population in a closed environment

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Abstract: Reindeer are not an invasive species by nature. However, introducing reindeer into a pristine environment with an abundance of lichen, the reindeer's favourite food, can have a devastating effect on the local environment if the herd population is not managed. This is mostly due to the slow lichen regrowth, decreasing the carrying capacity due to resource depletion. In these circumstances, a non-invasive species, like reindeer, can be considered as an invasive species whose actions threaten its own survival, because of its over utilisation of native resources.

We consider a population of reindeer, which were introduced in 1911 to St. George Island (one of the Pribilof Islands of the coast of Alaska). This was seen as an outdoor laboratory, with the population observed for forty years. As there was little hunting pressure on the herd and with no natural predators, this is considered as an almost closed system. The reindeer population grew almost exponentially in the early years of their being introduced, then started to decline, and eventually died out due to the lack of available resources; lichen reserves were exhausted over a 40 year period. Small amplitude oscillations in the reindeer population of St. George Island was noticed. Stable oscillatory behaviour is often observed experimentally. We hypothesise that these oscillations are due to the combined effects of gestation and maturation.

Accordingly, a single-species population growth model with a variable carrying-capacity is considered. The carrying-capacity is treated as a state-variable, representing the availability of a non-renewable resource (the lichen). We investigate a model based on the logistic equation where the rate of decrease of the carrying-capacity is proportional to the size of the population. We apply this model, with and without constant time-delays, to the reindeer population of St. George Island. The model that best fits the data includes a delay in the population and in the carrying-capacity. The estimated delay of 2.062 years coincides with the combined length of gestation and herd maturation.

Keywords: *Population modelling, invasive species, delayed differential equations*

1 INTRODUCTION

Understanding how population densities change with respect to time and space is central to mathematical modelling in population ecology. The logistic equation, though simple, is a key mathematical framework to explain population dynamics in the context of limited resources. Researchers have applied the logistic equation to different populations in an attempt to describe their dynamics. Early applications of the logistic equation, such as that by Pearl and Reed [1920, 1930] and Pearl *et al.* [1940], were to human populations. Since then the logistic equation has been utilised in many and varied fields [Banks, 1994].

The main shortcoming of the classic logistic equation is its assumption of a constant carrying capacity. Often the carrying capacity is viewed as a proxy for the state of the local environment (the availability of resources). The assumption of a constant carrying capacity may be valid in circumstances where the local environment is a constant (such as under experimental conditions), but this is rarely the case in nature. Further, implicit to this assumption of environmental constancy, is the assumption that the population embedded in the environment has negligible impact upon the ability of the environment to sustain it. To extend the applicability of the logistic equation, explicit time-dependent functional forms for the carrying capacity have been proposed. As an example, periodic functions were used to mimic the seasonal effects of the environment [Coleman, 1979; Lakshmi, 2003; Leach and Andriopoulos, 2004; Lakshmi, 2005; Swart and Murrell, 2007; Rogovchenko and Rogovchenko, 2009].

The logistic equation with a variable carrying capacity continues to play an important role in models involving variability in a local environment. Further developments in modelling population dynamics due to environmental stress now treat the carrying capacity as a state variable. This implies that the changes in the carrying capacity are described by a differential equations, just as is the case with the population itself. Such a model was presented by Safuan *et al.* [2013] which describes the growth of bacteria on healthy human skin under an occlusion.

The classic logistic equation is unable to exhibit any form of oscillation. In modelling the observed oscillations in *Daphnia* population data, Hutchinson [1948] incorporated a time delay into the classical logistic ordinary differential equation. This inclusion later proved fundamental in the development of delay differential equations (DDEs) [Arino *et al.*, 2006]. Delays involved with the process of reproduction, for example, are now known to cause oscillations [Kuang, 1993].

A thorough investigation of the dynamics of a number of important DDEs have been gathered by Gopalsamy [2013]. Some of these models represent examples of biological processes involving significant delays, such as a maturation and gestation period for animals and delays associated with regrowth or vegetative regeneration of plants.

Incorporating a delay in the carrying capacity was used to describe the often observed “punctuated evolution” in the growth of the world’s population. Yukalov *et al.* [2009] applied the idea of a delayed carrying capacity to analyse a scenario for which the present value of the carrying capacity is the result of the delayed influence of previous activities by agents. Forsyth and Caley [2006] applied a (discrete) delayed logistic model, along with three other models, to data for six different populations of reindeer and concluded that for three of the populations the delayed logistic equation provided a better fit.

Other equivalent forms of delayed logistic equations are discussed by Arino *et al.* [2006]. Moreover, a variety of DDE models for single species dynamics involving distributed delays, multiple delays and models with periodic delays are discussed by Ruan [2006].

2 DETERMINISTIC POPULATION MODEL

Our task is to model the population dynamics of reindeer (*Rangifer tarandus*) on St. George Island during the years 1911–1949 [Scheffer, 1951]. St. George Island is one of two islands (the other is St. Paul Island) that make up the so-called Pribilof Islands, located in the southern part of the Bering Sea. In the early 1900’s St. George Island had a well developed fur seal industry. In order to supply its residents with a sustainable source of meat, in 1911 the U.S. government released fifteen reindeer to the island – 12 females and 3 males. It was hoped that because of the abundance of lichen on the island the reindeer population would grow to supplement the dietary needs of residents [Klein and Shulski, 2011]. The importance of this population of reindeer is that their numbers were recorded almost every year until 1949.

The data provided by Scheffer [1951] is reproduced in Figure 1. In the absence of any natural predator on the island the reindeer numbers increased and within 11 years the population size reached 222 animals. After

this, rather than the population stabilising, it underwent a precipitous decline with apparent oscillations in the population. In 1950 the remaining reindeer were hunted to extinction. Huzimura and Matsuyama [1999]

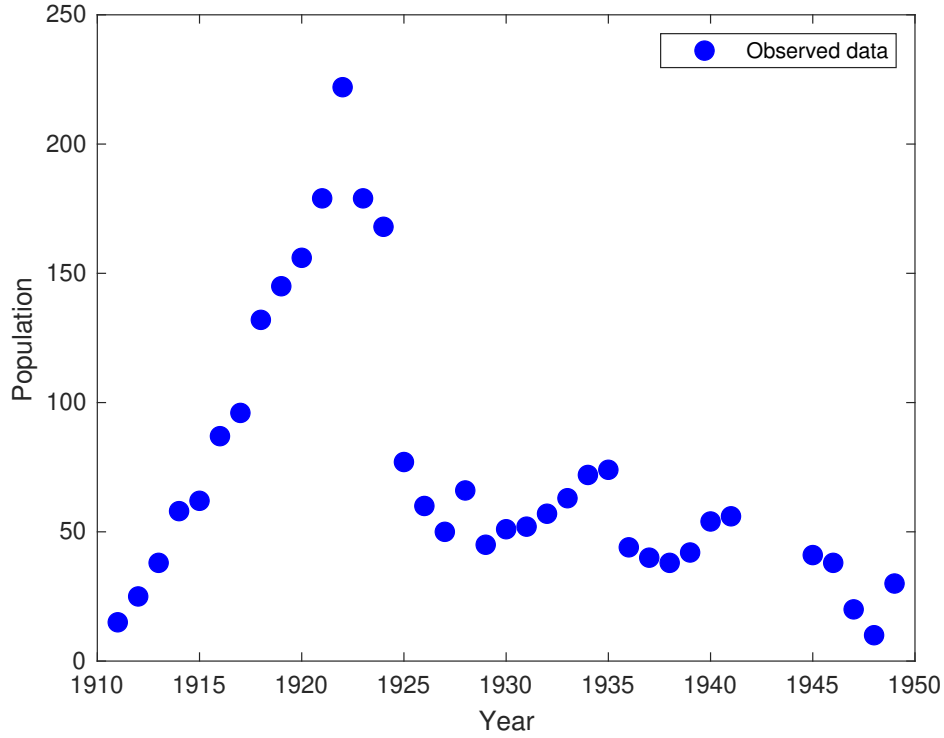


Figure 1. Reindeer population on St George Island from 1911 to 1949.

were first to model the population dynamics of the reindeer population. They proposed a logistic differential equation for the rate of change of the population with the following assumptions: (1) lichen is the primary food source for the reindeer; (2) the carrying capacity of the island depends on the available lichen biomass; (3) the carrying capacity decreases at a rate proportional to the size of population; (4) the reproduction rate of the lichen is negligible compared with its consumption rate by the reindeer; (5) the effect of harvesting is negligible. Taking these assumptions into account the Huzimura-Matsuyama (HM) model is

$$\frac{dN}{dt} = aN(t) \left(1 - \frac{N(t)}{K(t)} \right), \quad (1a)$$

$$\frac{dK}{dt} = -bN(t), \quad (1b)$$

where $N(t)$ is the size of the reindeer population and $K(t)$ is the carrying capacity at any time t . The parameter a denotes the intrinsic population growth rate whereas b is a measure of the consumption rate of lichen by the reindeer. If $a \neq b$, the above system of equations has an exact solution

$$N(t) = N_0 \exp(at) \left[1 - \frac{1}{a} (a - b) \frac{N_0}{K_0} (1 - \exp(at)) \right]^{a/(b-a)}, \quad (2)$$

with N_0 and K_0 being the initial population size and carrying capacity, respectively.

To find the parameter values a , b and K_0 that best fit the data, we use the sum of squares of the errors as the cost function, which we then have to minimise

$$SS = \sum_{i=1}^{36} [N_{\text{model}}(t_i) - N_{\text{observed}}(t_i)]^2$$

where t_i are the years of observation. Using the Nelder-Mead simplex method [Nelder and Mead, 1965], the three unknown parameters a , b and K_0 were estimated to be $a = 0.469$ (year^{-1}), $b = 0.0842$ (year^{-1}) and $K_0 = 229$ (reindeer). The sum-of-squares error was 23826. The fitted curve is shown in Figure 2. Although the model represents the data reasonably well for the first 9 years and capturing 70% of the maximum population in 1922 (222 observed compared to 156 for the fitted model), the lack of fit for subsequent years was not addressed by Huzimura and Matsuyama [1999]. The most obvious feature in the data is the apparent oscillations in the decaying phase of the population. It has previously been suggested that the introduction of time delays could capture this feature of the population dynamics [Ruan, 2006]. Following this advice we modify the HM model to include delays.

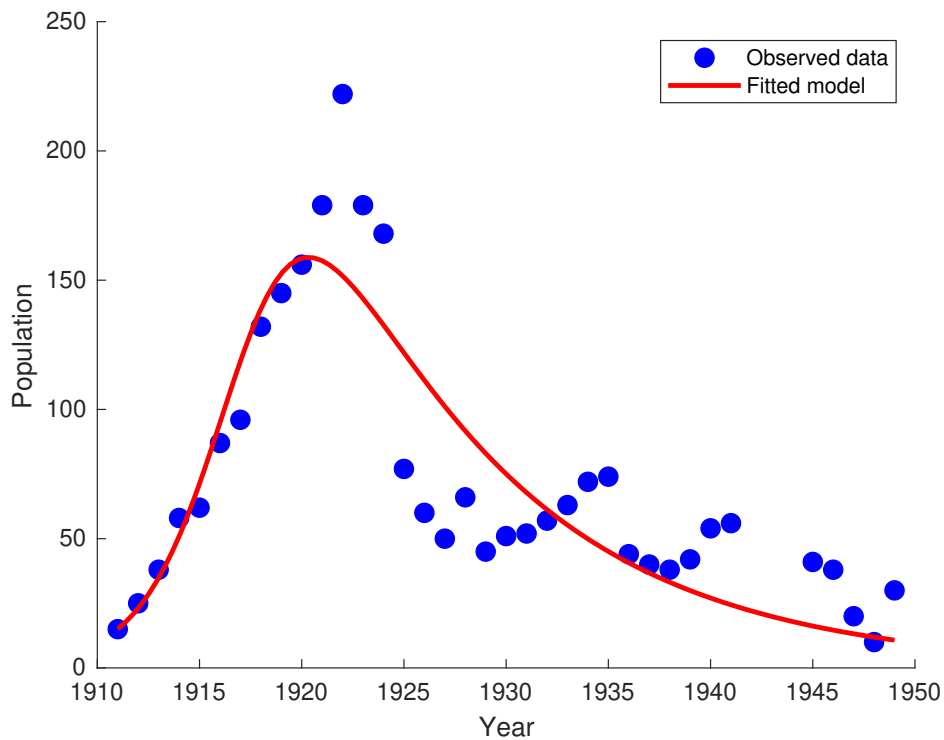


Figure 2. The Huzimura-Matsuyama model fitted using the reindeer population data.

In the HM model, the growth rate of reindeer depends on the total population size at any time t , thus excluding a potentially important biological process such as maturation or gestation, may have a considerable impact on modelling the reindeer. It can be argued that the growth rate should actually depend on the population size at some earlier time. Furthermore, the current state of the available lichen biomass is the result of a large number of prior interactions between the reindeer and the lichen resource, ability for lichen regeneration and earlier environmental conditions. The model proposed here considers these two phenomena by incorporating delays into the relevant terms.

3 DELAYED POPULATION MODEL

The HM model assumes the reindeer population is homogeneous and that each member of the population can reproduce at any time, t . A better model would be to include stage-structure by differentiating between adults and juveniles, for example. The nonlinear interaction that appears in such a model may naturally give rise to oscillations without the need to introduce delays, similar to predator-prey interactions. However, the data does not provide for such a breakdown of the reindeer herd. Going back to the HM model, there are two mechanisms describing the population growth: the birth rate and the effect of crowding.

The life-cycle of reindeer is not unlike many other mammals – conception, birth, a juvenile stage before entering adulthood. On St. George Island, breeding occurs in October wherein 90% of females will mate during this period. With good nutrition females give birth to a single calf each year (twins are rare). Calves are

born in May or June after a gestation period of about 7 months. Calves are weaned at about 3 months and rely on grasses for their nutritional sustenance, especially lichen. Reindeer sexually mature at 1–3 years (Ringberg *et al.*, 1981). Reindeer can live up to 20 years of age.

Given that we are not explicitly modelling a stage-structured population, only the adult population, we expect the value of the delay to have some meaningful interpretation. If we consider that the only important biological process is the maturation period then this value should be within the range of 1–3 years.

However, this interpretation may be too simplistic. Given the seasonal nature in the timing of breeding and birth, it is argued that the gestation period should also be included. It is certain that some of the adult reindeer that mated in October of the previous year may not have survived the coming winter months (February - April), thus the population of the reproducing herd should account for, which means we need to allow on average 7 months for gestation. The range in maturation is due to a number of factors including the sex of the reindeer as well as environmental conditions. For *Rangifer taranagus* on average the females mature at 18 months, whereas the males mature at 2.4 years. In reindeer, as with many other species, it is the dominant (thus older) males reindeer that mate. In fact they may mate with 5–15 females. The implication of this is that the ‘maturation of the herd’ is shifted heavily towards the average female maturation period. Hence, allowing for gestation and female maturation we postulate a delay about 25 months (2.08 years).

Using the ideas presented in Beddington and May [1975], we introduce a time delay into the system. The proposed model is

$$\frac{dN}{dt} = aN(t - \tau) \left(1 - \frac{N(t - \tau)}{K(t - \tau)} \right), \quad (3)$$

$$\frac{dK}{dt} = -bN(t). \quad (4)$$

The reindeer population at time t is given by $N(t)$ and $N(t - \tau)$ represents the number of reindeer at a time τ years earlier. We assume the delay τ is a fixed quantity that accounts for a complex set of biological processes, such as gestation and maturation.

The system indicates that the overall growth rate of the population is determined by the combined effect of reproduction expressed by the term $aN(t - \tau)$ and competition for available lichen expressed through $aN(t - \tau)N(t - \tau)$. It is not difficult to justify, based on recent studies, that aggressive interaction among reindeer functions to build and maintain social order and may restrict access to food resources to certain individuals or demographic groups within the herd [Donohue *et al.*, 2013]. The strength of this intra-species interaction is represented by the carrying capacity $K(t - \tau)$. Finally, the rate of change in the carrying capacity is due to the current reindeer population.

As before, we use the Nelder-Mead simplex method to best fit the observed data. A ensemble of one hundred initial guesses of the parameter values was taken. This was to avoid the finding of local optima, as often happens with the Nelder-Mead method. The parameter values found were $a = 0.557$ (year⁻¹), $b = 0.0754$ (year⁻¹), $K_0 = 213$ (reindeer) and $\tau = 2.062$ (years). The sum-of-squares error was 10067. From Figure 3, the delayed model captures the oscillatory nature of the data and 88% of the maximum population in 1922 (222 observed compared to 196 for the fitted model). The delay in the system of 2.062 years is close to the postulated delay, it being the sum of the gestation and maturation period of the herd. Although it could be argued that adding more delays to the system may give a better fit to the data, more delays in the system would be harder to justify from a modelling perspective.

Even though the delayed population model appears to give a better fit to the data than the HM model, we explore whether the difference is statistically significant. The HM model is nested inside the delayed model by setting the delay τ to zero. In general, if we have Model 1 (with p_1 parameters and a sum-of-squares error of SS_1) nested inside Model 2 (with $p_2 (> p_1)$ parameters and a sum-of-squares error of SS_2) and there are n observations, then the statistical significance of the difference between the models can be explained by the F-distribution F_{ν_1, ν_2} , where $\nu_1 = p_2 - p_1$ and $\nu_2 = n - p_1$ and the F statistic

$$F = \frac{\left(\frac{SS_1 - SS_2}{p_2 - p_1} \right)}{\frac{SS_2}{p_2}}.$$

In this case, we have $p_1 = 3$, $p_2 = 4$, $SS_1 = 23826$, $SS_2 = 10067$ and $n = 36$, giving $F = 5.467$ and $F_{\nu_1, \nu_2} = 4.15$ at the 5% significance level. Therefore, the difference between the delayed model and HM model is statistically significant.

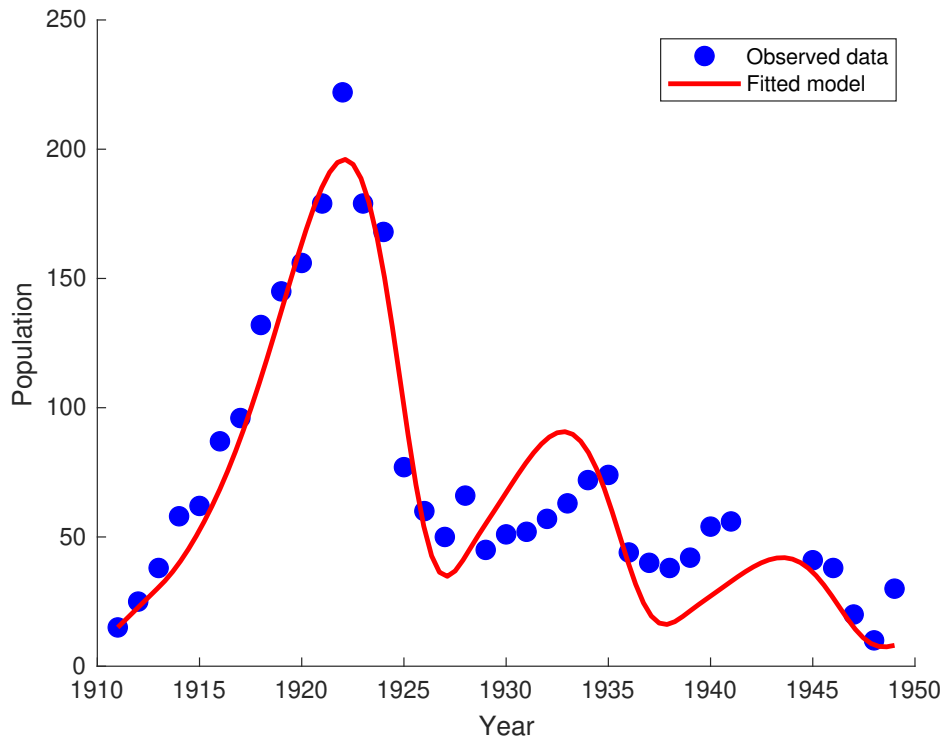


Figure 3. The delayed population model fitted using the reindeer population data.

4 CONCLUDING REMARKS

Delay differential equations play an important role in population dynamics and ecology generally, as there is often a delay (sometimes of significant duration) between the action of an animal and the response the action ensues. The inclusion of delays should be based on appropriate modelling rather than simply adding these in an arbitrary manner.

We have presented a comparison between the application of the HM model and its delayed version to a reindeer population on St. George Island between the years of 1911 and 1949. Unlike the HM model, the delayed model was able to estimate the timing of the population peak and its size, moreover it was able to account for the observed oscillations in the population data. We showed that the delayed model gave a significantly better fit to the data than the HM model.

The optimal delay was determined as $\tau = 2.062$ (years). A physical justification for the delay was advanced, it being the sum of the gestation and maturation period for *Rangifer taranagus*.

The model presented tries to account for inherent lags in the system, such as maturation and gestation periods. This allows for some of the transient shifts to be captured, at least when compared to a model without time lags. However, this model does not consider other factors that may change over time, such as the climate, which could influence the quality of the lichen food source, which in turn would affect the reindeer population. Furthermore, of the assumptions underpinning our model the assumption of negligible lichen regrowth is the more serious. Although lichen regrowth is a slow process, taking 10 to 15 years to replenish a region, it is a time interval well within the period over which the data was collected. The effect of lichen regrowth may play a vital role during the decay phase of the population. The model could be extended to include lichen regrowth as well as spatial effects by allowing for a heterogeneous distribution of lichen throughout the island.

Conservationists are increasingly faced with the challenge of mitigating species loss in a rapidly changing environment. Understanding when to intervene to ensure the survival of a species that's in decline is important as interventions are often very expensive. In relation to the reindeer data, any intervention when the population is at a local minimum (around 1927) might be more expensive compared to the same intervention when the population is at a local maximum (around 1934). A management policy of deferring an intervention must be based on a sound understanding of the relationship between the reindeer and its environment. Given that

environments are subject to random changes in climatic conditions an important direction for future work is to extend the current model to also include stochastic processes.

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