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Forward hysteresis and backward bifurcation caused by culling in an avian influenza model

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A B S T R A C T

The emerging threat of a human pandemic caused by the H5N1 avian influenza virus strain magnifies the need for controlling the incidence of H5N1 infection in domestic bird populations. Culling is one of the most widely used control measures and has proved effective for isolated outbreaks. However, the socio-economic impacts of mass culling, in the face of a disease which has become endemic in many regions of the world, can affect the implementation and success of culling as a control measure. We use mathematical modeling to understand the dynamics of avian influenza under different culling approaches. We incorporate culling into an SI model by considering the per capita culling rates to be general functions of the number of infected birds. Complex dynamics of the system, such as backward bifurcation and forward hysteresis, along with bi-stability, are detected and analyzed for two distinct culling scenarios. In these cases, employing other control measures temporarily can drastically change the dynamics of the solutions to a more favorable outcome for disease control.

1. Introduction

H5N1 (highly pathogenic avian influenza) has rapidly spread among wild and domestic bird populations in recent years. With increasing frequency, the virus has shown the ability to infect mammalian species which are in close contact with infected birds [1–5]. Most notably, over 600 humans have contracted H5N1 since 1997 with a reported 60% mortality rate [6,7]. The most serious public health threat that H5N1 poses to humans is the potential appearance of an extremely virulent human-to-human transmittable strain of avian influenza [8–12]. Reducing the probability of this occurring requires strong control measures. However, avian influenza is a complex disease, infecting multiple species of animals, which creates difficulties in tracking and controlling the disease. Hence, control has been directed at reducing incidence among poultry populations, since these are the main animal populations responsible for transmitting the disease to humans.

One of the main control measures applied to poultry is culling, i.e the targeted elimination of a portion of the poultry population in areas affected by avian influenza, to save the rest of the birds and reduce the possibility of further outbreaks. Wide-area (mass) culling has been successful for isolated outbreaks. However, mass elimination of poultry becomes too much of an economic burden in areas of wide-spread outbreaks and in countries dominated by smallholder farms. As the number of infected increases above a threshold level, it has been suggested that control measures be shifted from mass culling to a modified strategy. The modified strategy includes elimination of only infected flocks and high risk in-contact birds along with other control measures [13,14]. In areas with backyard poultries, the selective culling of only infected and highly exposed flocks is often employed instead of mass culling, even for small outbreaks [13–16].

Mathematical modeling provides a way of understanding the complex epidemiology of avian influenza and can yield valuable insights on how different control strategies impact the disease dynamics. There have been several authors who have looked at culling in particular. Le Menach et al. analyzed a spatial farm-based model, which treats poultry farms as units, and found that an immediate depopulation of infected flocks following an accurate and quick diagnosis would have a greater impact than simply depopulating surrounding flocks [17]. Martcheva investigated the efficacy of culling in comparison with other control measures, and determined that culling without repopulation is the most effective control measure based upon sensitivity analysis [18]. Iwami et al. investigated a mathematical model for the spread of wild and mutant avian influenza, and explored the effectiveness of the prevention policies, namely elimination and quarantine policy [19–21]. Shim and Galvani evaluate the effect of culling on the

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host-pathogen evolution [22]. Impulsive systems have also been considered for modeling culling, which will be discussed further in Section 2.

Even though mathematical and statistical models have been focused on culling as a control strategy, almost no special attention has been put on how culling strategies differ from region to region as a result of socio-economic factors. In this article, we model avian influenza dynamics in domestic birds under the control measure of culling, giving special attention to these different culling strategies. We incorporate, into an SI model, various culling rates that are functions of the number of infected birds in the population.

For certain culling rates in our model we find complex bifurcations, namely backward bifurcation and forward hysteresis. In epidemiological models with backward bifurcation, the disease may persist even though the basic reproduction number, $\mathcal{R}_0$, is less then 1. In this case, as $\mathcal{R}_0$ approaches unity from the left, there exist endemic equilibria in addition to the locally stable disease free equilibrium. This leads to bistable dynamics: If the initial number of infected individuals is small enough, the disease will die out; if, however, the disease level is above some threshold, then the disease will persist. Backward bifurcations have been found and explored in several models from mathematical epidemiology [23–28]. On the other hand, forward hysteresis has rarely been detected or studied in epidemiological models. Forward hysteresis refers to the existence of multiple endemic equilibria and bistable dynamics when $\mathcal{R}_0 > 1$. In this case, although the disease will always persist, there can be a dramatic difference in the asymptotic level of disease, depending on the initial conditions. Hu et al. recently studied an SIR model with saturating incidence and piecewise defined treatment, which they showed to exhibit forward hysteresis [29].

Bistable dynamics can have important implications for control. During the onset of an outbreak, actions can be taken in order to “drive the solution” to the region of attraction corresponding to a low level equilibrium or disease free state. For example, a temporary reduction in transmission rate can produce this shift in asymptotic dynamics. Temporary control measures such as enhanced biosecurity and movement ban on poultry have the impact of reducing the transmission rate and, hence, may be important in ultimately bringing the disease under control.

In Section 2, we introduce our general model, derive the reproduction number $\mathcal{R}_0$ for the general model, analyze the general model, and describe the distinct culling functions that we will incorporate into the system. In Section 3, we consider the case of mass culling as an example. In Sections 4 and 5, we give the motivation behind employment of modified culling and selective culling, incorporate the corresponding culling rates in the system, and analyze the resulting models. In Section 6, we consider the implications of the bistable dynamics observed under selective and modified culling and present numerical simulations which highlight the impact of temporary control measures. In Section 7, we conclude with a discussion about our results and their implicaations.

2. Modeling culling in avian influenza H5N1

The first model of H5N1 influenza was introduced by Iwami et al. [30,19,20]. The model does not explicitly take into account any control measures. In practice, culling infected and exposed poultry has been utilized in order to reduce the global spread of H5N1. We alter the basic avian flu model in birds to explicitly involve culling as a control measure. Since culling is applied only after an outbreak has occurred, we assume that the culling rate depends on the number of infected individuals. The general model takes the form:

$$M: \quad \begin{cases} \frac{dS}{dt} &= \Lambda - \frac{\beta IS}{N} - \mu S - c_S\phi(I)S, \\ \frac{dI}{dt} &= \frac{\beta IS}{N} - (\mu + \nu)I - c_I\psi(I)I \end{cases} \tag{2.1}$$

with nonnegative initial conditions : $S(0),\ I(0) \geqslant 0$. The state variables S and I represent the number of susceptible domestic birds and the number of infected domestic birds, respectively. The total number of domestic birds is denoted by N, where $N = S + I$. For the parameters, Λ is the recruitment rate of domestic birds, β is the transmission rate, μ is the mortality rate of domestic birds, ν is the disease-induced death rate for birds, and c_S and c_I are the culling constants for susceptible and infected birds respectively. We assume susceptible domestic birds S are culled at a rate $c_S\phi(I)$ and infected domestic birds I are culled at a potentially higher rate $c_I\psi(I)$. The culling functions $\psi(I)$ and $\phi(I)$ are assumed to be nonnegative continuous functions (see Table 1).

Our choice of modeling culling as a continuous function dependent on the number of infected, I, reflects our aim to consider different culling strategies in which culling effort depends on I, i.e. increases, decreases or non-monotone with respect to I. Impulsive systems can also been considered for modeling culling. An advantage of modeling culling as a pulsed process is that culling does not occur continuously through time. Terry [32] considered an impulsive system to model culling of crop pests, where the culling occurred as pulses applied at fixed times. However, employment of culling at fixed times may not be realistic for avian influenza since it ignores the fact that culling occurs as a response to outbreaks. Another possibility is state dependent impulsive models, which was considered for pulse vaccination in an SIR model [33]. In this approach, impulsive culling would occur upon I reaching a threshold value, but culling effort would not vary beyond this impulse switch and limited qualitative results can be obtained in such a model. A limitation of our model is that culling occurs as a continuous, ongoing process, which may not be realistic. There are advantages and disadvantages to each modeling approach, but considering continuous culling rate functions dependent on I, as in system (2.1), may help to better understand the dynamical consequences of the different culling strategies mentioned in the Introduction.

2.1. Analysis of general model

The solutions of (2.1) are non-negative for all time t. Moreover, there is a positively invariant compact set

$$K = \left\{ (S, I) \in \mathbb{R}^2 : S \geqslant 0,\ I \geqslant 0,\ S + I \leqslant \frac{\Lambda}{\mu} \right\}$$

in the non-negative quadrant of $\mathbb{R}^2$ which attracts all solutions of (2.1). Indeed, by adding the equations in (2.1), we see that $N' \leqslant \Lambda - \mu N$. Hence, for any solution $(S(t), I(t))$,

Table 1
Definition of the variables in the modeling framework.

Variable/Parameter	Meaning
S	Susceptible domestic birds
I	Birds infected with HPAI
Λ	Birth/recruitment rate of domestic birds
β	Transmission rate of HPAI among domestic birds
$\phi(I)$	Culling rate for susceptible poultry
$\psi(I)$	Culling rate for infected poultry
c_S	Culling coefficient for susceptible poultry
c_I	Culling coefficient for infected poultry
μ	Natural death rate of domestic birds
ν	HPAI-induced mortality rate for domestic birds